THE BREEDING BIOLOGY AND BEHAVIOUR OF EUDYPTES PENGUINS

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PART I

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P R E F A C E.

This thesis is in two parts. The first consists of 7 chapters made up of a short introduction and 6 papers either published, in the press, or in preparation, (Warham, 1963; 1971c; 1972; in press a. and b; and ms.) dealing with the biology of the individual species. The second part is a general review and discussion of particular aspects of the biology of these penguins based partly on the data given in the species accounts and partly on additional material.

The objectives of the study were to uncover details of the main events during the breeding and moulting cycles of the various species of Eudyptes or crested penguins, and to describe their behaviour patterns. Most of these birds nest at great distances from centres of civilisation and consequently the work involved organising and undertaking visits to remote islands. These included Antipodes Island (6 weeks in 1969); Campbell Island (3 weeks in 1969); Macquarie Island (15 months in 1959-1961) and Snares Island (3 to 6 weeks in 1967, 1968 and 1969). Field assistants collected additional data at Snares Island in 1969, 1970 and 1971.

Partly because of the remoteness of the breeding places and the different times spent there, the amount

and kind of data collected has varied from species to species. Thus while the information for E. chrysocome was based on daily observations over two breeding seasons, that for E. sclateri was mostly gained during only 6 weeks study at the nesting places. Similarly work on E. pachyrhynchus was undertaken over 6 seasons but, although the birds were observed at intervals from their arrival to their departure after the moult, observations could never be sustained for long periods. On the other hand, the parallel study of E. atratus was done over 5 seasons but with sustained observations only during the 4 months between chick raising and the annual moult. At the time of writing it has still not been possible to observe these birds from their arrival to the time of hatching of their eggs. This will be rectified in the 1972/73 breeding season.

Not withstanding such logistic problems, these crested penguins have proved rewarding subjects and despite the uneven coverage, the general outlines of their breeding systems have been established and the main behavioural repertoire, hitherto mostly unrecorded, has been set down. The new information contained in the thesis is too varied and numerous to list in detail. Before this study there had been no accurate and complete accounts of the annual cycles of and behaviour of any member of the genus. The present work will, it is hoped, go some way towards recti-

fying the lack of ecological information regarding New Zealand and Australian penguins about which Stonehouse (1967; p. 32) laid particular stress.

C O N T E N T S

PART I.

PART II.

CHAPTER 1.

INTRODUCTION: THE GENUS *EUDYPTES*.

CHAPTER 1.

INTRODUCTION: THE GENUS EUDYPTES.

1.1. General.

The Eudyptid or crested Penguins comprise a group of medium-sized, flightless sea-birds inhabiting the Antarctic and cool temperate waters of the Southern Ocean. They breed mainly on islands, usually in large aggregations. Most nest close to the shore but colonies are quite often found well inland and up to some 150 m above mean sea level.

In these birds maturity is delayed, and few birds probably breed before they are 5 years old. Having obtained a partner and attained breeding age nesting occurs annually. The eggs are usually laid in the spring and summer months. There is a strong tendency for pair-bonds and nest-sites to be retained from year to year. Two dissimilar-sized eggs are laid but only one chick is reared. The breeding system is noteworthy for the long stints at the nest undertaken by the two sexes in turn, during which the on-duty bird fasts. The chicks are guarded for about 3 weeks by the males, after which the chicks leave their nests to aggregate in creches and both parents are freed to bring food.

Following the fledging of the young birds the breeders return to the sea where they remain feeding and acquire

the sub-dermal fat stores that are drawn on during the annual post-nuptial moult. This takes place at the nest where most partnerships are again re-formed. During the 3 to 4 weeks needed to replace the old feathers completely, the birds again fast and lose weight steadily. Having acquired the new plumage the birds return to the sea and do not reappear at their nesting places until the beginning of the new breeding season.

As befits highly sociable species, crested penguins have a complex vocal and visual communication systems. Their voices are raucous and far-carrying, show considerable intra- and inter-specific differences, and the accompanying displays are usually dramatic and eye-catching.

These birds are active on land but when at rest their body temperatures are low compared with those of most other birds. Cloacal temperatures of 35 adult E. pachyrhynchus average 37.6 ± 1.1°C and those of 9 adult E. sclateri averaged 38.6 ± 0.3°C as against a mean value of 40.8°C for 81 species of birds given by McNab (1966). Low body temperatures are also recorded for other penguins (summary in McNab, loc. cit) and for their nearest relatives, the Procellariiformes (Warham, 1971a). The birds in these two groups share the ability to lay down big energy reserves as sub-dermal and depôt fat. These reserves enable them to fast for long periods and if, as seems probable, the birds' basic metabolic rates are also

low, reduced resting temperatures may be adaptations for conserving energy during those parts of the annual cycle when fasting is necessary. The low temperatures may also be a primitive character.

Crested penguins support a varied fauna of ecto-parasites. Although outside the compass of the present study, the known ticks, fleas and chewing lice associated with these birds are discussed and tabulated in Appendix 1 to Chapter 8.

1.2. Nomenclature and Taxonomy.

The crested penguins comprise a genus of five or perhaps six species as follows:-

Rockhopper Penguin E. chrysocome (Forster, 1781) = E. crestatus (Miller, 1784).

Fiordland Crested Penguin, E. pachyrhynchus Gray, 1845.

Snares Crested Penguin, E. atratus Finsch, 1875.

Erect-crested Penguin, E. sclateri Buller, 1888.

Macaroni Penguin, E. chrysolophus (Brandt, 1837).

This arrangement maintains the Fiordland, Snares and Erect-crested Penguins as distinct species. Sometimes these are treated as merely three subspecies of E. pachyrhynchus. However, the present investigation has confirmed that each is distinct morphologically and that although their ranges outside the breeding season overlap

to some extent, their breeding distributions are allopatric with asynchronous breeding cycles and no evidence of interbreeding. Full discussions of the evidence for regarding each as a separate species are included in the accounts of these birds in Chapters 4 and 5.

The taxonomic position of the Royal Penguin, however, treated here as the subspecies schlegeli of the Macaroni Penguin, is not so clear. The Royal Penguin breeds only at Macquarie Island and its treatment as only subspecifically distinct follows the usage of Carrick and Ingham (1967; 1970). The relationship between these two forms requires clarification, as apart from the Macaroni being slightly smaller, particularly in the beak, the morphological distinctions are imperfectly known and more information is needed based on statistically valid samples of breeding birds from different populations. The two forms show some overlap in the facial characters which are the main outward evidence of their distinctiveness. Thus most Royal Penguins have cheeks and throats that are white or grey in colour whereas in typical Macaronis these areas are covered with black or dark grey feathers. Very occasionally white-faced birds breed among the Macaronis (Downes et al. 1959) and black-faced ones among the Royals (Falla, 1937; Keith and Hines, 1958). The latter may take partners of the normal facial type and produce eggs and perhaps young (Warham, 1971b). It

is not clear whether the birds showing the extremes of facial colour pattern represent the extremes of the range of variation within the particular populations or whether they are members of the one form that have straggled to the breeding places of the other. It would be very surprising, given the known propensity of crested penguins to turn up far from their birthplaces, if some Macaronis did not reach Macquarie Island and some Royals places like Heard and Kerguelen Islands where they would be expected to associate with the resident Macaroni Penguins.

In view of these uncertainties I have chosen to follow Carrick and Ingham in regarding the Royal Penguin as only subspecifically distinct from the Macaroni, although judging by the rarity of Macaroni-type birds at Macquarie Island and Royal-type ones at Heard Island, even if these proved to be immigrants from elsewhere, the amount of introgression seems likely to be so small that a good case could be made for giving the two forms full specific rank. A study of the genetics of the facial patterns in the Royal Penguin is in preparation (P. Shaughnessy, *in litt.*).

Oliver (1953) put forward reasons why the name of the Erect-crested Penguin should be changed from *schlegeli* to *atratus* which in turn would require the abandonment of *atratus* for the Snares Crested Penguin. This he proposed calling *robustus*. His proposals have been accepted by

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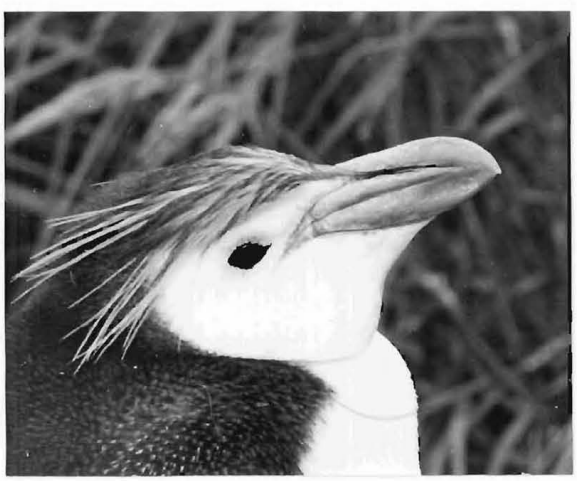
d



e

f

a. Erect-crested Penguin
E. sclateri

b. Rockhopper Penguin
E. chrysocome

c. Fiordland Crested Penguin
E. pachyrhynchus

d. Snares Crested Penguin
E. atratus

Royal Penguins
E. chrysolophus schlegeli

e. White-faced variety (common)

f. Black-faced variety (rare)
Very similar to typical race.

FIGURE 1: HEADS OF EUDYPTES PENGUINS.

some authors e.g. Richdale (1957) and Stonehouse (1967) but not by others e.g. Falla et al (1966) and Kinsky (1970). None of these nor any other author has published a critical assessment of the information on which Oliver based his arguments. This has been attempted in the account of the Snares Crested Penguin (Chapter 5) where my reasons are set out for rejecting Oliver's proposals and for retaining the original and well established names used here.

1.3. Species Characteristics.

Eudyptids range in size from the Rockhopper, standing about 30 cm high, to the Royal Penguin about 48 cm high. Within an age class the males are larger than the females particularly in the bill. The birds are all dark on the back and head and white below with black soles to their otherwise flesh-white feet and reddish-brown bills. The species differ mainly in the forms of their crests and in details of the feathering of the face and throat (Figure 1). These differences doubtless provide important inter-specific recognition characters as first noted by Wilson (1907).

The Rockhopper (Figure 1b) has a narrow yellow superciliary stripe starting well back from the base of the bill. Just behind the eye the stripe gives rise to long filamentous feathers which form a series of drooping

tassels on either side of the head. Most of these tassels are yellow but some are black. Shorter, more upright black feathers extend across the back of the crown as an occipital crest. The eyes are of a bright geranium red colour with more of an orange cast than is seen in the eyes of other crested penguins.

The Fiordland Crested Penguin (Figure 1c), also known as the New Zealand Crested Penguin (in Australia as the Thick-billed Penguin), has a broad sulphur-yellow supercilliary band which arises near the nostril and extends backwards as a crest. This may either droop at the rear or extend sideways like a fan. There is very little development of an occipital crest in this or any other species except the Rockhopper. Furthermore, unlike other Eudyptids, the bases of the bill plates are not fringed with pale fleshy fillets but with dark and inconspicuous skin. Another feature is the way in which the dark feathers of the cheeks are often parted to show their white bases as a series of pale diagonal stripes. The eye colours of breeding birds vary from grey brown to a dull claret while occasionally birds having eyes of a bright vermillion hue may be seen.

The Snares Crested Penguin (Figure 1d) is very like the Fiordland species but has a heavier bill conspicuously edged by pale coloured fillets. The supercilliary band tends to be narrower than that of the Fiordland species

but it is similar in form and origin although the crest is a little longer than that of the latter bird. The eye and bill colours are also similar in these two species but it is rare for Snares Penguins to show white streaks on their cheeks because the bases of the feathers in this region are normally dark.

The Erect-crested Penguin (Figure 1a) is slightly taller than the two previous species; its yellow crest, arising from a broad superciliary band, tends to be upturned rather than drooping although these birds have more control over their crests than most other Eudyptids and at times flatten them to their crowns. The superciliary band often appears to arise towards the gape, lower down than it does in Fiordland or Snares Crested Penguins. The bill is also straighter with less bulbous lateral plates and both the bill and eyes are of a browner colour than those of other Eudyptids of breeding age. Flippers and tail are long and the underflipper pattern is a diagnostic and bold pattern of blue-black on white. The head, cheeks and nape are a rich velvety black, not bluish black as in other dark-faced Eudyptids.

The Macaroni Penguin (Figure 1e and f) has a quite distinct type of crest and adults lack a well defined supercilliary stripe. Instead, a series of orange coloured filamentous feathers arise from a central orange-yellow patch on the forehead. Some of these plumes project

backwards while others dangle down on either side of the face. The head, cheeks and throat are blackish often shading into grey below the eyes. There is usually a small yellow patch on the lores and an area of white on the rump. Royal Penguins are similar but have white, grey or dark grey cheeks and heavier bills than the Macaronis. Macaroni and Royal Penguins were formerly separated from other penguins in the genus Catadyptes Mathews, on account of their distinctive crests and because they usually have 14 rectrices as contrasted to the 16 possessed by other crested penguins.

In all the species young birds before their first feather moult at about 12 months old ("yearlings") are readily recognisable, but those of most other age classes resemble the adults in their general appearance (Figure 2b) Chapter 5). It is possible that growth does not cease with the attainment of adult plumage and that, for example, very big-billed males are very old birds. Not enough re-measurements of marked birds have as yet been made to establish at what age bill growth ceases.

Unless a study population is composed of banded birds of known age, it is not possible to determine the precise status of the penguins in adult plumage, that appear on the colonies but have neither eggs nor chicks. Most such birds will be "sub-adults" or "pre-breeders" - birds that have not attained sexual maturity - or "pre-

vented breeders" - birds physiologically capable of breeding but prevented from doing so by external factors - to use the terminology of Carrick and Dunnet (1954). But some such birds will be breeders that have lost eggs and chicks i.e. "failed breeders". When the exact status of such birds is unknown I have used the term "non-breeders" to include all these categories.

1.4. The Literature of Eudyptes.

It is only in recent years that the biology of these birds has been subjected to detailed study. Richdale (1941; 1950) published the first major papers solely devoted to the breeding biology of a crested penguin. They were based on observations of a lone pair of E. sclateri nesting atypically on the mainland of New Zealand. Pettingill (1960) reported observations on Rockhoppers at the Falkland Islands and Stonehouse (1971) on work on the Snares Crested Penguin with special reference to sexual dimorphism. The most detailed investigation, a long-term study of the population dynamics of the Royal Penguin, is as yet unpublished although some preliminary information has been given (Carrick, 1964; Carrick and Ingham, 1967; 1970).

Many other sources of information on the biology of these birds exist. It is appropriate to start with the information about the Rockhopper and Macaroni Penguins

given by Murphy (1936) as he provided a masterly review of the state of knowledge at that time of their habits, distribution and status and he included many extracts from the reports of expeditions and sealers. Falla (1937) and Roberts(1940) gave additional information on the same species. Hagen (1952) and Paulian (1953) dealt with the Rockhopper Penguin at Tristan da Cunha and Kerguelen respectively. Richdale included descriptions of the behaviour and breeding of Eudyptids in his monographs on sexual behaviour in penguins (Richdale, 1951) and on penguin populations (Richdale, 1957). Gwynn (1953) discussed egg sizes and incubation periods in Rockhopper and Macaroni Penguins while Rand (1955) gave a brief account of the Macaroni at Marion Island. Elliott (1957) in his study of the birds of Tristan da Cunha, included data on the Rockhopper Penguin additional to those given by Hagen. Downes, Bailey, Gwynn and Young (1959) brought together four years of studies of the birds of Heard Island and included valuable data on the breeding of the Rockhopper and the most detailed account of the breeding timetable and behaviour of the Macaroni Penguin at present available. Bailey and Sorensen (1962) assembled information on the two breeding Eudyptids of Campbell Island - the Rockhopper and Erect-crested Penguins - and provided many illustrations of these birds and of their breeding colonies, while Swales (1965) outlined the

breeding cycle of the Rockhopper at Gough Island. Stonehouse (1967; 1970) dealt with all the crested penguins in his reviews of the Spheniscidformes with particular reference to their distribution and problems of heat balance. For general accounts of Australasian species reference should be made to Oliver (1955), Falla, Sibson and Turbott (1966) and Serventy, Serventy and Warham (1971).

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CHAPTER 2.

THE ROCKHOPPER PENGUIN, *Eudyptes chrysocome*,

AT MACQUARIE ISLAND.

THE ROCKHOPPER PENGUIN, *EUDYPTES CHRYSOCOME*, AT MACQUARIE ISLAND

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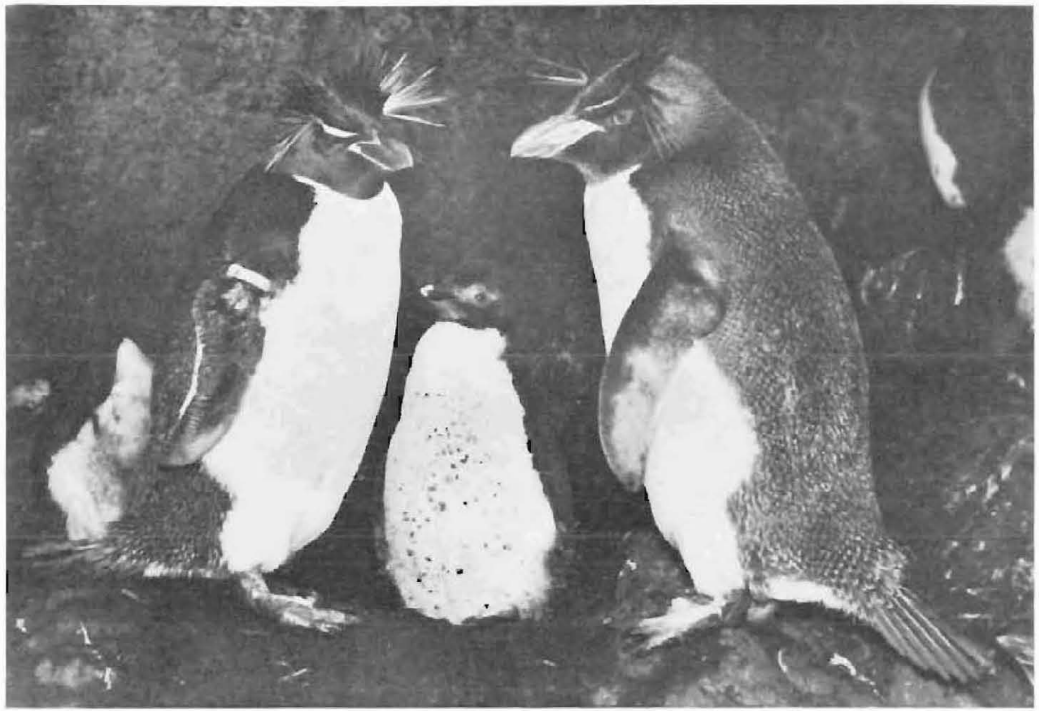

Rockhoppers and their chick. The female is on the left and the chick is 31 ± 1 days old.

THE ROCKHOPPER PENGUIN, *EUDYPTES CHRYSOCOME*, AT MACQUARIE ISLAND

JOHN WARHAM*

ORNITHOLOGISTS and other biologists have found most of the sub-Antarctic islands of absorbing interest. They provide resting and breeding places for many colonies of birds and mammals and, by their isolation from the larger centers of civilization and the main marine transport routes, constitute part of a vast, natural wildlife sanctuary. Unique opportunities for scientific work present themselves here to naturalists interested in observing the life and habits of numerous species of flying birds, penguins, and seals which spend varying proportions of the year swimming in the surrounding ocean or flying over it in search of food.

The Australian National Antarctic Research Expeditions (ANARE) have established stations at two sub-Antarctic islands, namely Heard Island and Macquarie Island. The writer was a biologist with ANARE at the latter station and carried out field work there from 29 December 1959 to 12 March 1961.

Macquarie Island lies at latitude 54°30′S and longitude 159°E. It has been briefly described by the author (Warham, 1962) and in detail by Law and Burstall (1956). Here the large colonies of Rockhopper Penguins (*Eudyptes chrysocome*) are mainly found on the rocky west coast. Because these colonies adjoin and to some extent intermingle with those of the Royal Penguin (*Eudyptes chrysolophus schlegeli*) and because of their location amid talus debris, it is not possible to estimate the island's total Rockhopper population, but it must be of the order of some hundreds of thousands of birds. Most of the larger rookeries spill over into those of the Royal Penguins in this way, the latter occupying the more level and open areas between boulders, while the main body of Rockhoppers breeds higher up in niches and among tussock grass. Rockhoppers do not nest

* Member, Australian National Antarctic Research Expedition, Macquarie Island, 1960–1961.

at the edges of the inland rookeries of Royal Penguins; these are far higher than any Rockhopper colony on the island. On the east coast there are small colonies on most rocky points: a group at Garden Cove, about five minutes walk from the ANARE station, was used for the present study.

The Rockhopper stands about 30 cm high and has straw-colored and drooping superciliary crests. It is a penguin of the sub-Antarctic zone of surface water and breeds also at the Falkland Islands, at Tierra del Fuego, Tristan da Cunha and Gough Island, Marion Island, the Crozets, Kerguelen, Amsterdam Island and St. Paul Rocks, Heard Island, and at the Auckland and Campbell islands south of New Zealand (Murphy, 1936: 416). It is present at the breeding stations only during the spring, summer and autumn months, the precise wintering areas at sea being unknown, though presumably lying in the sub-Antarctic zone.

At Macquarie Island the species had not previously been studied in detail, but in 1949 A. M. Gwynn (1953) investigated egg laying and learned the length of the incubation period. In 1957, 75 pairs of adults were flipper-banded by M. P. Hines. Previous accounts of the species are those of Murphy (1936: 415–431), Falla (1937: 87–94), Hagen (1952: 12–35), and Elliott (1957: 554–556).

Rockhopper Penguins, like other members of their genus, are readily sexed by bill size. Males have larger and deeper bills than females. Falla's conjecture (1937: 87) that the sexing of birds collected at the island by the Australian Antarctic Expedition of 1912–1913 was mistaken, because some small-billed birds were labelled as males, is undoubtedly correct. Males are also heavier than females. Sixteen pairs weighed on 30 December 1960, gave averages of 2.7 kg for the males (range, 2.1–3.2) and 2.5 kg for the females (range, 2.0–3.2). Only one female was heavier than her mate. These differences would probably have been greater if weighings had been made later in the breeding cycle, for on 30 December breeding males have been ashore fasting for about 25 days and their weights must be below normal, whereas their mates have been going to sea daily and should be in better condition. Sexing was particularly easy when both members of a pair were together (Frontispiece) and was confirmed by behavior at copulation and by a display used only by males. Only one instance of reversed coition was noted (proved by subsequent dissection) and even here the birds had been correctly sexed on bill size and display. Examination of the cloaca as used by Richdale (1951: 88) was not necessary and would have been inadvisable owing to the risk of egg loss to Southern Skuas (*Catharacta skua*).

METHODS

Very few Rockhoppers have been banded at Macquarie Island as chicks, and the present account is not based on a community of known age structure. The data are the result of regular observations of about 30 pairs, most of which were flipper banded in January, 1960, as breeding adults. A few were marked in early November the same year.

The bands were of aluminum and of a type developed by A. M. Gwynn from those used by W. J. L. Sladen at the Falkland Islands for other penguins. Each was stamped with a two-letter combination. These bands seemed quite satisfactory but the early ones, of soft metal, started to be lost through breakage after about three years' wear.

When re-sighting, the positions of each bird's feet were marked directly with a ball-point pen on a photograph of the rookery and the band letters added. These data were later transferred to a master photograph, and the writing on the duplicate erased with acetone. Once the penguins had settled down to breed, each next nest site was given an identifying letter on the photograph.

In winter, in the birds' absence, a blind was built overlooking the colony. This blind protected observers from bad weather during long watches and also protected the birds from undue disturbance. Tame though they are, penguins tend to behave abnormally if the observer is not concealed, a point emphasized by Richdale (1957: 44).

Visual records of behavior were supplemented by motion pictures, subsequent frame-by-frame analysis being made later in Australia.

BREEDING CATEGORIES AND IMMATURES

All penguin and petrel communities appear to include large numbers of birds that do not breed. The Rockhopper community is considered as being composed of the following categories:

(a) Successful breeders, age unknown. These, which had mostly reared chicks during the previous season, usually re-mated with their previous partners and reoccupied their former nest sites.

(b) Failed breeders, age unknown. Many of these were believed to be inexperienced birds, which, as Richdale found in *Megadyptes antipodes*, tended to lose their chicks or eggs through lack of attentiveness, and in whom the pair bond was weaker than in established breeders. Failed breeders also include older birds that lost their eggs or chicks through misfortunes of various kinds.

(c) Non-breeders, birds in adult plumage with fully developed crests. These were either lone males or were pairs occupying nest sites or birds without nests which appeared from about 5 December onwards.

(d) Immatures:

i. Yearlings. R. Carrick collected a very short-crested bird on 11 December 1957, known from its band to be a yearling; the many similar, rather small and subdued birds that come ashore about mid-December are believed to have been of the same age. Their bills and eyes were dull brown in color. It has been established by many ANARE biologists that yearling Royal Penguins return as dull-billed, short-crested birds at a year old and the probability is that similarly short-crested Rockhoppers are of the same age.

ii. Probable two- and three-year-olds. Many birds had short but quite prominent crests which were bushy and not pendant. By analogy with *E. chrysolophus*, whose plumes are mostly fully developed at three years old, it seems likely that these Rockhoppers were two years of age.

iii. Chicks. Born between 17 and 28 December, these left the island between about 24 February and 10 March and did not return until mid-December.

THE ANNUAL CYCLE

Successful breeders.—In 1960 and 1961 most of the males in this category arrived between 18 October and 1 November. They went straight to the nest sites which they had occupied the preceding March at the molt and were joined by their previous mates 0 to 14 days later. The eggs were laid from 7 to 18 November and, after one long incubation span by each sex, hatched between 17 and 25 December. The chicks ceased to be guarded between 6 and 16 January, huddled together in crèches, and left the island between about 24 February and 10 March. Concurrently their parents also went to sea to "feed up" in preparation for the annual molt. These birds returned from 23 March to 18 April to stand on their nests. Molting started about 2 to 8 April and finished about 19 April to 5 May. After a further 2 to 9 days ashore they departed for their winter at sea. Successful breeders are discussed in detail below.

Failed breeders.—In the study area containing 30 pairs, 7 failed to breed. One pair, OX and WT, laid two eggs in a nest profusely lined with grasses—the work mainly of the male—but soon allowed both to be lost. OX went to sea at once and the female WT followed two days later. Both reappeared three weeks afterwards and for about a fortnight were seen near or at their nest. Then WT was found with a new male at nest site Z. Shortly after this, OX appeared at his nest with a new unbanded female. OX and WT now wandered independently and stood in various nests in the absence of their rightful owners during the crèche stage of the chicks. The two birds did not rejoin. Indeed, WT was seen copulating with an unbanded male on 29 January while OX stood only a short distance away. Both WT and OX disappeared in early February and OX was not seen during the subsequent molt. He did, however, breed in the following year at a new nest. WT returned to molt at the same time as the successful breeders and did so with an unbanded male on site Z where she bred the next season.

Birds that lost their eggs after incubating them for some time left the colony for 0 to 14 days and then returned to stand in pairs at their nests. They showed an increasing tendency to wander and to take up new positions as these became vacant. Thus pair C, who lost their egg around 14 December, were both present daily to 11 January, i.e., right to the start of the crèche stage. At this time all failed breeders left the

colony but many returned intermittently in the evenings from mid-January until early March when chicks and parents departed. Pair AB, who failed to hatch their egg, continued incubation, rather erratically, for 14 more days. Even when the eggs disappeared the pair remained at their nest until the general daytime exodus of the breeders, which was complete by 16 January.

Non-breeders.—An unbanded pair at site Z, and a lone male, WB, were ashore from the start of the season until the end of the guard stage, apart from about 14 days when the breeding females were incubating. SB did not attract a mate until 21 December when a temporary attachment was formed with a newly arrived female VV. From then until 7 February, when he disappeared, this male had several temporary partners but he seemed unable to keep them. At this time, too, the pair bond of the birds at site Z started to weaken. They had been very active in display, but parted company on 7 January and were not identified again. WB returned to its chosen spot the following year, gained a mate and the pair produced an egg.

During the incubation and guard stages the aggressiveness of the nest holders prevented newcomers from gaining footholds in the colony. Only those birds like WB and the pair at Z, which arrived early, maintained their positions there. Few other non-breeders were ashore until 5 December, by which time incubation was well advanced. Now, long-crested birds that had not been seen before, started to occupy places vacated by failed breeders. This penetration increased until, with the absence of the successful breeders at sea by day, the newcomers wandered at will over the rookery. They acquired partners and stood on nest sites as though they were the rightful owners. The males harried the chicks, pecking them severely and driving them from place to place. These non-breeding birds began to molt in the last week of February and by the end of that month most had returned to sea.

Immatures.—The yearlings and medium-crested birds were first noted about 10 December. Their numbers gradually increased until, like the non-breeders, they were able to find positions inside the rookery. The yearlings were very silent and self-effacing, dominated by all other Rockhoppers except by the chicks, and these the yearlings sometimes attacked vigorously. Some of them formed liaisons with non-breeders, with other immatures and even with chicks, but such liaisons did not last long. About 16 January some of the yearlings started to molt and completely molted birds were present by 31 January. Thereafter, the numbers of all classes of immatures decreased until by the end of February very few remained. They did not reappear that season. Barrow, quoted by Murphy (1936: 431) states that at the Falkland Islands the one-year-olds

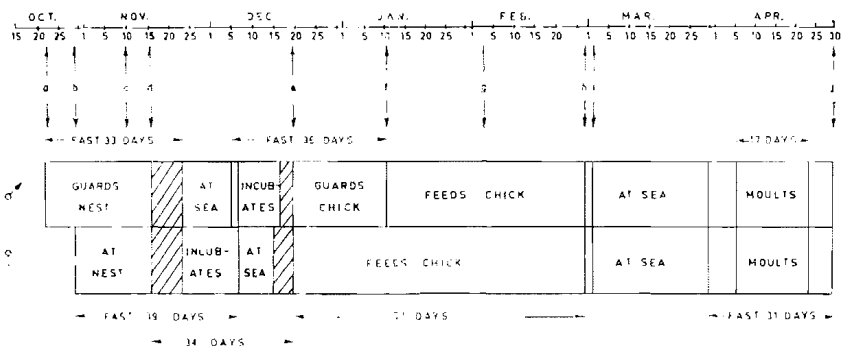

Figure 1. Diagrammatic cycle of successful breeders from arrival to molt.

arrive with the returning adults for the annual molt, but this did not occur at Macquarie Island.

The Cycle of the Successful Breeders

The full cycle of a representative pair is shown in Figure 1.

Return.—The first Rockhoppers to appear in the spring of 1960 and 1961 were males that had bred the previous season. After a short pause on the rocks to preen, these birds climbed to the nest sites where they had molted five and one-half months before. The first birds were seen both in 1960 and 1961 on 15 October. The season has apparently not changed in the last 50 years, for the 1911 party also saw their first birds on the same date (Falla, 1937: 94). This is interesting in view of Elliott's (1957: 556) suggestion that at Tristan da Cunha the species arrives about a fortnight later than formerly. In 1960 the first marked bird reached the Garden Cove colony on 18 October but the inflow was greatest from 21 to 24 October when 13 out of 23 marked males were first sighted.

There was some wandering about the rookery by the earlier males but, as soon as their numbers built up, each remained on its nest. Elliott's statement that the newly arrived males appear to have no attachment to any particular site does not accord with the present findings, nor with the behavior of other penguins of the genus.

The females returned from 24 October to 3 November, 0 to 14 days after their mates. The mean difference based on 23 records was 6.5 days. Most of these females immediately joined their mates, but some, of unknown origin, formed temporary attachments with males whose own mates were delayed, or perhaps never arrived. However, in all instances where the females had been marked previously, such substitute partners were ousted when the regular ones appeared.

C O R R I G E N D A

ANARE Reprint BZ/107

"The Rockhopper Penguin, Eudyptes chrysocome, at Macquarie Island"

by John Warham

The Auk, Vol. 80, No. 3, 30 July 1963, pp. 229-256.

p. 223, par. 2, line 3; SB should read WB

p. 234, Figure 1: The legend should read:

Figure 1. Diagrammatic Cycle from Arrival to Molt. (Cross-hatched sections are periods where adults change duties frequently).
(a) male returns (b) female returns
(c) first egg laid (d) second egg laid
(e) eggs hatch (f) chick enters crèche
(g) chick's first feather appears
(h) chick departs (i) parents depart
(j) parents leave for winter sojourn at sea.

Nest occupation to egg laying.—On the evening of 2 November the colony appeared to be full and on the following days the first copulations were noted, though coition may have started before this date. The interval between the arrival of the female and the laying of the second eggs was 17, 17, and 21 days in the only instances where both dates were known. Laying began on 8 November and was complete by 18 November. Most eggs were seen between 11 and 16 November. An egg at Raine's Point on 31 October must have been laid nearly a week sooner than the normal date at which first eggs are seen at Macquarie Island. Once the eggs were laid copulation ceased between the nesting pairs.

The first small egg was not incubated but either adult stood over it, the other bringing grasses or stones which were set on the edge of the nest. Mutual display was fairly frequent but the rookery was not very noisy during this period. Change-over on the egg occurred often, accompanied by the shoulders-hunched attitude. No bird was known at this time to feed and it is unlikely that any did so, for usually both birds were present during the daily check. On the morning of 12 November three nests were guarded by single birds but the missing partners all reappeared while the colony was under observation. Only one, a male, was wet. It had probably been bathing in a rock pool.

Incubation.—Incubation did not start until the second egg was laid. This large egg was given priority and was the first to be tucked into the incubation pouch following a change of guard. The incubation period was determined by Gwynn (1953: 2–6) who gives useful data on the length of time between chipping and hatching and of the effect of removing one or both eggs. Re-laying did not occur. He showed that the smaller egg was viable and that, if the big one was lost, the small one could take its place effectively. His three accurate determinations of the incubation period were 33, 34, and 34 days. Three further determinations, accurate to one day, made during the present study, were 34, 33.5, and 32.5 days. No three-egg clutches were seen in 1960, although such have been recorded, and they are common at Tristan da Cunha.

The start of incubation was marked by one bird squatting in the nest in the prone position. The eggs were rested on the upper parts of the webs and tucked into the deep incubation pouch which exists in both sexes. Although some males incubated sporadically in the early days, the females were more persistent, and by 20 November the first of the males left for the sea. The remainder disappeared gradually until by 26 November only females were incubating and all but two were alone. The period between the males' arrivals and their return to the sea was 25 to 39 days. For 19 records the mean was 33 days. Deviations from the mean were mostly due to differences in the dates of arrival.

The colony was now very quiet. Some females threatened the occasional non-breeders that entered the rookery, others were more receptive. Thus the lone male WB now moved about, preened the heads of several incubating females, and was sometimes preened by them. Attacks on sitting birds by non-breeding males were also seen; the response was the submissive attitude described below. The feces of the sitting birds were greenish or yellowish, indicating the absence of food in their stomachs. Many nestings failed in this period. Thus, on 29 November, the egg at nest V was found uncovered and the female VB, which had been incubating, was seen coming up from the rocks with her plumage wet; she had apparently gone to bathe, leaving her eggs unguarded and, by the following evening, both eggs and bird were missing.

The feeding period at sea for the males lasted from 9 to 17 days and averaged 12 days for 25 determinations. The first relief of a female was noted on 1 December, 5 days before the next male appeared. By 10 December all the females had been relieved and were back at sea. They had been ashore for 33 to 45 days, averaging 39 days (20 records) and had been incubating for 10 to 19 days, averaging 14.5 days (20 records).

The time elapsing between the male's arrival and his assumption of incubation varied. Some females seemed reluctant to relinquish their eggs. WA, whose mate arrived on 9 December, did not leave until the night of 12–13 December, although she changed guard soon after his arrival. When the males came in, a greeting ceremony with mutual trumpeting took place, and for some hours afterwards the newcomers were recognizable by the cleanliness of their plumage and feet.

The colony was again quiet while the males incubated. Strangers now got a severe drubbing if they came within pecking range and there were no assaults on sitting birds. The males' spells ranged from 8 to 16 days, averaging 10.5 days for 21 determinations and their nest reliefs occurred between 14 and 21 December.

During rainy periods the rookery became a quagmire. Eggs and adults became encrusted with mud but most of the eggs hatched and there was no obvious tendency in favor of drier sites.

Hatching. The eggs hatched from 17 to 25 December. Each female was back before her egg started to chip; usually she was present two days before the hatch. Her stay at sea varied from 7 to 13 days and averaged 8.5 days from 21 determinations. During the hatch both adults remained on duty and there were fairly frequent changes on eggs or chicks, the shoulders-hunched attitude being struck at nest relief. The tiny chicks rested on the feet of the parents and were effectively blanketed by the thick feathers on either side of the incubation pouches.

Gwynn (1953: 3) showed that normally only one egg is hatched and

that, because the smaller egg was not covered until the bigger one was laid, the latter hatched first even when both were incubated. Often the small one was ejected from the nest before the big one started to chip. Both might hatch and some of the study pairs had two chicks. No pair reared more than one. A. Gourin, medical officer of the 1954 ANARE party, weighed a few chicks from hatching to the end of the guard stage: he found that the smaller chick died from two to five days after birth, its maximum weight being about 156 g. The weight at birth was about 75 g.

The guard stage.—From hatching until the time when neither parent remained with the chick a new routine was established. The males were always at their nests whenever the colony was inspected. This was done morning and evening, sometimes after dark, and on 28 December a continuous watch was made from 0300 to 2000 hours. No evidence was gained that any male left the rookery to feed, although one was seen to leave the nest for a short period when its mate was present, apparently to bathe.

The excreta of the males was white as contrasted with the pinkish mutings of birds that had been feeding. The males now brooded during the morning while their mates came ashore, perhaps as early as 0800 hours but mostly in the afternoon. By 1800 hours both were present, the females covering the young and the males standing nearby. The females were gone before dawn, leaving the males on guard. This routine began one to five days after the chick was first seen and was general by 25 December.

The end of the guard started about 6 January when a chick was first seen to leave its nest; by then several others were too big to be brooded. By 16 January the guard stage was over and neither parent was present during the morning inspections. The length of the males' periods on guard varied from 21 to 30 days and averaged 26 days (21 determinations). The total length of the males' second fasts ashore, varied from 31–40 days and averaged 36 days (21 determinations).

The crèche stage.—The chicks left their nests when from 19 to 23 days old, apparently of their own volition, sought the company of other chicks, and huddled together in small crèches. On entering the crèches they weighed 825 to 1,070 g, averaging 907 g (4 records by A. Gourin), and had not started to "shed down." This is a much shorter guard period than obtains with some other penguins; e.g., in *Megadyptes* it is from 35 to 53 days (Richdale, 1957: 40). Pettingill (1960: 216) gives two records suggesting that, at the Falkland Islands, crèching in the Rockhopper starts at 13 days of age, all his 9 chicks being in huddles by 16 days from hatching. This is appreciably shorter than at Macquarie Island,

Figure 2. Adult about to feed fully feathered chick.

but Pettingill did not know the dates of hatching and merely estimated his chicks to be six days old at the start of his observations.

From one to three days after the chicks vacated their nests the parents began to spend the day at sea. This allowed the non-breeders and molting immatures then ashore to take up positions in the colony, where they formed temporary attachments and defended the places where they stood as if they had been present since the start of the season. Male parents, on returning, usually ousted such intruders without difficulty but some females were unable to do this. They were attacked and perhaps even prevented from feeding their chicks (see also discussion under bowing display below).

Feeding of the young was now done in the late afternoon, in the evening, or after dark (Figure 2). Inspections were mostly made in the evenings and no sustained watches were undertaken. However, numerous sightings of chicks being fed by banded adults proved that both parents were feeding, that some chicks got meals from both on the same day, and that the same parent might feed its chick on successive days. Each chick received about two visits every three days. There was no evidence that the parents kept together at sea and they were seldom seen together at the nest. If one appeared while the other was present, the normal ceremony, with loud trumpetings, signalled the event.

At first the crèched chicks were not venturesome. In heavy rain or sleet, or if spray was blown into the colony, the young penguins turned their backs to the weather and huddled together often with one flipper across the back of a neighbor. Others clustered beneath rocks. The huddles were often broken up by aggressive non-breeders but some of these preened the chicks.

Many chicks supplicated from non-breeders, whose reactions varied: some vigorously pecked the young ones away; some bent down as if bewildered by the chicks' impatient tappings against their bills; some throbbed and even opened their beaks as if to feed the supplicant, but despite close observation none was ever seen to do so. No chicks were observed begging from short- or medium-crested Rockhoppers nor did they display as Sladen describes in the chick of the Adélie Penguin (*Pygoscelis adéliae*).

As the chicks grew they begged from strangers less often. They became more independent and began to stand on their nests if these were vacant. They were now less tolerant and fought one another mildly, tilting their heads to one side in threat, pecking and using their flippers. Some also helped their parents to evict intruding chicks. The composition of the crèches varied from hour to hour as their members moved around, and as the birds became stronger the crèches gradually dispersed. If frightened, they quickly huddled together again and they were always more timid than the old birds.

On arriving at the nest, their plumage sleek and wet from the water, parents usually first adopted the shoulders-hunched posture, then bowed and finally trumpeted loudly forward or perhaps vertically. Some males gave the male display. One or more chicks, peeping loudly and waving their flippers, then left the crèche and approached the parent. If several appeared the adult brusquely pecked off all the young except its own. The latter begged by wobbling its head and by pecking at the sides of the adult's bill and at its belly and flanks. Some were so eager that they tried to insert their bills into those of the parents as these bowed into the nest. Some parents, mostly females, needed little inducement before they disgorged. They might even open their beaks to enclose those of the chicks when they were not begging—as they did during the nestling's early days before it was strong enough to supplicate properly. Others needed persistent stimulation before they disgorged, when they often delivered small meals. Occasionally a penguin appeared not to recognize its young one and pecked it. The latter, accustomed to assaults from the non-breeders, continued to beg until its importunity eventually gained it a meal.

The chicks' "see-up" calls, which, unlike those of the Adélie (Sladen,

1958: 36), did not seem to alter appreciably from birth to departure, ceased only when food was actually being passed. The bill remained inside that of the parent for four to six seconds and a series of meals was delivered. Thus the male at nest M gave 19 meals between 1615 and 1624 hours on 23 January; the male at nest O gave 25 meals between 1720 and 1736 hours on 8 February; and the female, nest W, gave 10 meals between 1625 and 1643 on 15 February, despite interruptions from non-breeder WB and his current partner, both trumpeting whenever she fed her chick. On the other hand, the female, nest L, gave only 5 meals on 18 February despite the chick's continued supplications.

Food was spilled in feeding, so that chicks that had been fed and the parent responsible were often identifiable by the pink stains on their breasts or by food adhering to their gapes. The pinkish color of the food and feces at this stage apparently came from pigment in the crustacea on which the adults were feeding.

Pettingill (1960: 215) marked 10 family groups and saw two chicks fed by their own parents after crèching had begun. This appears to be the first indication that the chicks are not fed communally at this stage. Pettingill's conclusions were confirmed by experiments made at Macquarie Island where nine of the chicks were marked with colored collars shortly before the end of the guard stage. After they had entered the huddles these chicks were seen on 29 occasions to be fed by their own banded parents. None was ever seen to get a meal from strange penguins or to be fed anywhere but on or near the appropriate nest site. The so-called "guardians of the crèches" are, of course, merely the non-breeders already discussed. These seem to be concerned solely with guarding their own persons or those of their partners, and showed only a passing interest in the chicks. Many other unmarked chicks were fed by banded birds and again there were indications that these were the rightful parents. No banded bird was ever seen to feed more than two meters from its nest. This routine held right up to the last meals seen to be given, when many chicks had already gone to sea.

Pettingill was doubtful whether chicks that were large enough to leave the crèches were still fed by their parents. He reports seeing fully-grown young fed at great distances from their nests and noted at least one instance where an adult responded to begging regurgitation, then continued farther inland where it again fed a large chick. No such incidents were seen at Macquarie Island and, although chicks often begged from adults not their parents (but adults that sometimes opened their beaks and appeared to feed), no food really passed. Close observation was needed and, as Pettingill does not mention this behavior in non-breeders, it is possible that he was misled by their actions.

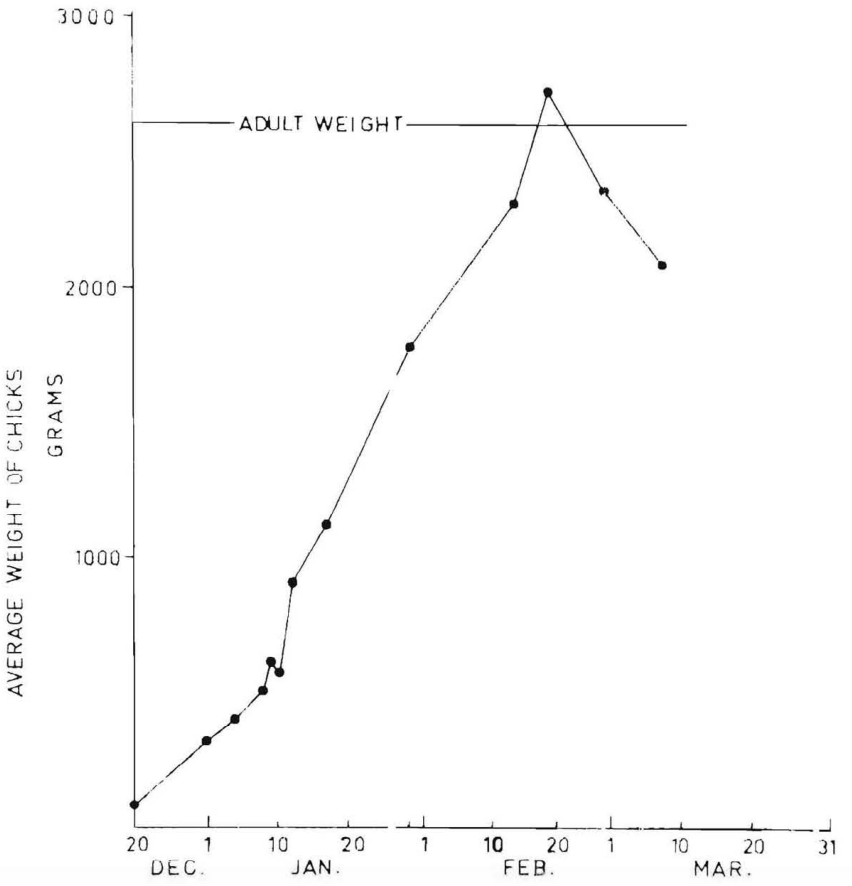

Figure 3. Average weights of Rockhopper chicks during 1956 (after K. Keith).

Sladen (1958: 60–61), who showed that the parents of the Adélie chicks fed their own young throughout, saw only two instances of parents feeding chicks other than their own. In both, the young were on nest sites and supplementary to the rightful chicks. With the King Penguin (*Aptenodytes patagonica*), which also feeds only its own chick (Stonehouse, 1960: 40–43), "mock-feeding" occurs between non-breeders, or adults without food, and chicks. Stonehouse notes that such behavior cannot easily be distinguished from true feeding.

Rockhopper chicks were not weighed in the study as they were easily frightened and might have been lost in deep holes between rocks, but Figure 3 shows the average growth curve made from weighings taken in 1956 by the ANARE biologist, K. Keith. The rapid growth to more than

adult weight, followed by a decline to fledging, should be noted. This decline may be partly due to the high energy demands accompanying feathering but, from direct observation, it seemed that the weight of food given during the last fortnight of the chicks' stay ashore declined. Even if there was no slackening of the parents' visits—and this cannot be gauged from the data obtained—there was certainly a curtailment in the time spent feeding the chicks. Furthermore, as already noted, the females were hindered from feeding by the non-breeding males still present.

After a series of meals many chicks still supplicated. The parents tried to escape; they climbed onto a rock to preen, the chick followed, the parent descended again to the nest, and so on. Many parents now pecked their young but seldom succeeded in subduing them. Some escaped by going back to sea. Usually the old birds did not stay long in the colony after feeding but some remained to stand on their nests preening themselves or their now satiated young.

On 29 January feathers were seen on the tips of one chick's flippers. By 6 February tail feathers were also visible on several birds. On 11 February some had shed all their down except for tufts on the mantle, the nape and at the bases of the flippers. By 18 February most had lost all their down apart from a little on their napes, crowns and the roots of the flippers, and faint superciliary stripes were visible. A few had stripes as distinct as in the yearling birds.

About this time the young Rockhoppers began violent flipper exercises. A few birds seemed to become demented, vibrating their flippers to and fro at high speed and, dancing across the rookery, collided with adult birds. Such chicks appeared to be unaware of the pecks they received and they employed the same flipper actions as used under water, the flippers often touching at the top of each stroke.

The chick's departure.—The first chicks left about 24 February, and near the larger colonies small mobs congregated on the rocks below the nesting areas. Few chicks were seen to set off. One marked chick left aged 71 ± 1 days old and others left at 67 ± 2, 72 ± 1, and 70 ± 1 days old.

A chick on the rocks on 6 March had to climb a line of boulders heavily embedded in kelp from which it was repeatedly washed backwards by the waves. Eventually the chick got through to the open sea but only a strong and healthy bird could have done this. Similar hazards face many of the young penguins as thick kelp beds encircle the island.

It was not discovered whether the young were deserted by their parents, but four banded birds visited their nests after their chicks had left. This suggests that there is no desertion period.

Discussion of the breeding cycle.—An interesting feature of the breed-

ing routine is the female's assumption of the first incubation shift. It might have been expected that after laying she would go to sea to "recuperate," this being the rule with Adélie, King, and Yellow-eyed penguins, and with many petrels. But the Rockhopper is not alone in this behavior, for Macaroni and Royal penguins behave similarly. Whatever other benefits this arrangement conveys, it seems that a system whereby the male can take charge of the chick up to the crèche stage is important. The male is far more vigorous in defense of the nest site than the female and is not intimidated by the non-breeding infiltrators. If the female were on duty during the guard stage it seems likely that many nestings would fail through interference.

Stonehouse (1960: 55) reproduces a graph showing the monthly variations in surface plankton in sub-Antarctic waters based on samplings made from the research vessel Discovery and drawn from Foxton (1956). This graph shows a peak of plankton in December, a fall in January, and a sharp rise to a high level extending throughout February into March. Foxton also emphasizes that at 160°E the plankton in January, 1938, and February, 1936, was typical of the summer months in other regions, with most of the organisms concentrated on the surface and with very high plankton counts in February. If similar variations in the foods taken by the Rockhopper Penguin apply at Macquarie Island—and there has been no comparable sampling there—then the division of labor between the sexes during the incubation and rearing stages may be correlated with such variations.

Hatching occurs when the plankton supply, as given by Foxton's graph, is almost at a minimum; the weight of food needed for the chick is also very small and it seems reasonable to expect a single parent to make good its fast and collect sufficient additional food to nourish the chick during the guard stage. From the time of hatching onwards, the plankton graph climbs steeply until, by the crèche stage, the food situation is excellent. Both adults are now feeding and adequate food should be available for them and for the rapidly growing chick now demanding big meals. Indeed, with several millions of penguins fishing local waters and coming ashore daily to tend their young, the food supply now must be approaching superabundance. When adults and chicks finally leave in early March the plankton curve is still at a high level and, though about to decline, remains high until mid-March. The chicks therefore go to sea while there is still plenty of food in local waters.

Most recent students of penguins have concluded that parents recognize each other and that chicks recognize their parents. Mated Rockhoppers can certainly identify each other at distances of several yards and, as has been shown, recognize their chicks after they have entered a crèche.

Richdale (1951: 229), thought that in *Megadyptes* adult birds rely on visual clues but that appearance and voice differences are involved in parent–chick, chick parent recognition. Sladen (1958: 73) thought that visual means are most important with the Adélie, but Stonehouse (1960: 41) provides evidence suggesting that the King Penguin chick recognizes its parents by their calls. In the Rockhopper both visual and auditory clues appear to be used and it is perhaps significant that the writer was able to identify several of the study birds by peculiarities of voice, behavior, or posture. Presumably such differences are even more apparent to the birds' mates and neighbors. On the other hand, the chicks' voices seemed very uniform to human ears and the writer could not identify individuals by their voices. That auditory means are used is suggested by the way in which adults feed chicks on dark nights when appreciation of small differences of posture or appearance seems impossible.

The occupation of the colony by non-breeders during the crèche stage and the formation of temporary partnerships may have a bearing on pair formation. Although the ages of such birds were unknown, many must have been nearly mature so that their attachment to particular partners and to particular places could provide a basis for successful breeding in the following season. This might also be one reason why nest sites left unoccupied by previous tenants at the start of a season were promptly occupied by other pairs: these could be pairs formed when at the site as "second tenants" during the crèche period the year before.

Display and Posturing

Penguins of the genus *Eudyptes* have more displays than the pygoscelid penguins. Many of the behavior patterns described by Richdale for *Megadyptes* as "love-habits" (Richdale, 1951: 15–34) seem to have counterparts in the present species, but a direct comparison is difficult with the available descriptions.

Both Murphy (1936: 416) and Roberts (1940: 215) state that Rockhopper Penguins can erect the yellow superciliary plumes and do so during fear and rage. This ability was not noted on Macquarie Island. Some voluntary movement of the black occipital crests was evidently possible, though they were normally kept erect, but there seemed to be no muscular control of the drooping yellow tassels of the adult birds. Nor were the eyes capable of great changes as in the Adélie Penguin, although the irides do contract and dilate, perhaps according to emotion, as others have noted.

Displays of a Sexual Nature

Mutual preening.—This activity was seen between mated birds whenever they were together and it frequently followed more vigorous display.

The birds turned their heads to one side and nibbled each others' throats and necks with the tips of their bills. Between mated birds such actions seemed to have sexual significance but the same movements were also seen between most other categories of Rockhoppers in or out of the breeding season. Non-breeders that formed attachments always preened their partners and mutual preening followed when a bird allowed another of the opposite sex to join it for the first time. Chicks were preened by their parents and *vice versa* and this may have helped to curb excessive begging.

Stone-carrying.—The placing of stones around the nest had some practical value in reducing losses caused by eggs rolling down the slopes, but the formal manner in which stones, grasses, and earth were laid down suggested that such actions had a deeper significance. Much stone-carrying was done by the males in the laying period when their mates were on the nests. The females took the offerings from the edges of their nests and placed them to one flank with a quivering movement. Following a change of guard on the egg, many males hurried to and fro in search of stones or grass, sometimes tearing the latter from the tussocks, before they departed. Stone-carrying was seen whenever the birds were ashore, even during the molt.

Quivering.—A nesting bird bent down and, with bill slightly ajar, shook its head rapidly from side to side while pointing into the nest or moving its head from flank to flank. The flippers were not lifted and the movements were either conducted in silence or accompanied by deep repeated *kruk kruk* calls. The crests became blurred because of the head movements. The bill might be empty during quivering, but more often grasses and the like were simultaneously placed to one flank, the bird either sitting or standing. Both sexes quivered, sometimes in unison. Most displays were initiated by the males and then might lead to more intense activity or might follow mutual or trumpeting displays. Quivering was seen mainly at the nest but, during the molt, birds which shifted from their places and took up temporary positions elsewhere until the disturbance was over were seen to quiver and bow. WB, a male non-breeder in 1960, also quivered occasionally.

Bowing.—With its bill near its feet, the penguin uttered a succession of deep, throaty, throbbing notes while its body shook in time with the calls. The head was not shivered, as in the last action. Bowing display was used by both sexes and as solo or dual performances when both reached forward with their bills together (Figure 4). Many such displays faded out but others led to male display or mutual display and the latter always seemed to begin with bowing. When two birds were together the bowing and throbbing of the one usually triggered similar behavior in the other. This was why females were so easily distracted from feeding their

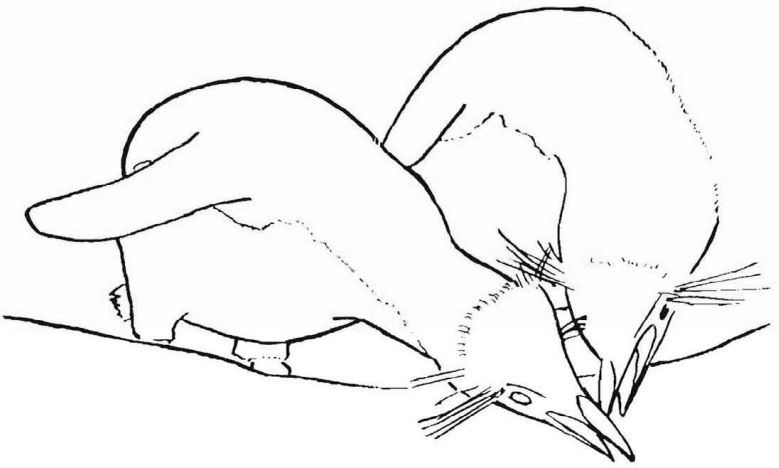

Figure 4. Bowing display.

young if neighbors bowed as the females bent down to disgorge. The latter then seemed unable to resist bowing in response; as some onlookers bowed whenever a female nearby bent down to feed, serious interference resulted.

One example from many will illustrate this. On 4 February 1961, a female returned to a rock overlooking her nest and made regurgitating movements towards the chick that emerged from a crèche. Two birds on an adjoining site, male OX and his partner, both non-breeders, showed great interest, cocking their heads to one side and throbbing towards the parent whenever she started to disgorge. She responded each time by display and never succeeded in delivering any food. Soon OX jumped up and drove her away, and when the chick switched its begging to OX, it was ignored. The female went back to sea shortly afterwards.

Shoulders-hunched attitude.—In the action the body was fairly upright but the head was tilted forward so that the bill pointed down. The shoulders were peculiarly hunched with a kink showing at the back of the neck. The flippers were held stiffly forward and downward at about 30° to the vertical with their inner surfaces parallel and facing each other (Figure 5).

This distinctive stance was used by a bird returning to its nest in the absence of its mate. When a few paces off, the penguin adopted this posture and, on reaching the nest, padded around with a quaint mincing gait, pivoting on its feet. Usually it held the shoulders-hunched posture for several seconds before breaking into loud trumpetings. At nest relief during incubation the bird relinquishing the egg moved off silently in this way. Its mate, similarly hunched, then stepped forward and took over.

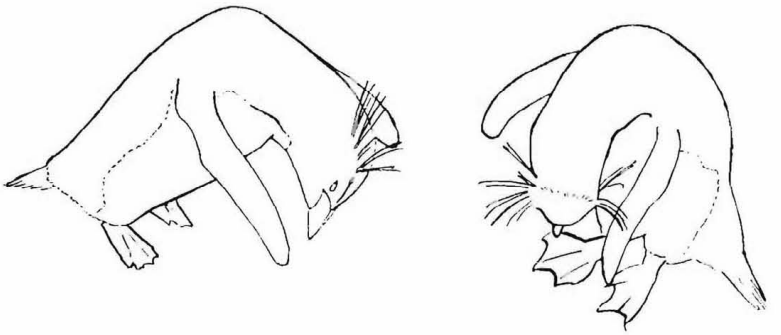

Figure 5. Aspects of the "shoulders-hunched" posture adopted on arrival at the nest.

The shoulders-hunched posture was also adopted by the male immediately after coition when he stood quite still before shaking his head and preening.

Trumpeting.—See Figure 6, Left. Typically, as a relieving bird approached its nest, both it and its mate broke into loud trumpeting with their opened bills reaching towards each other. Neighbors often joined in, directing their yells towards the newcomer. When the latter stepped into the nest the pair switched to vertical trumpeting or perhaps to the mutual display described below. In vertical trumpeting the beaks were pointed

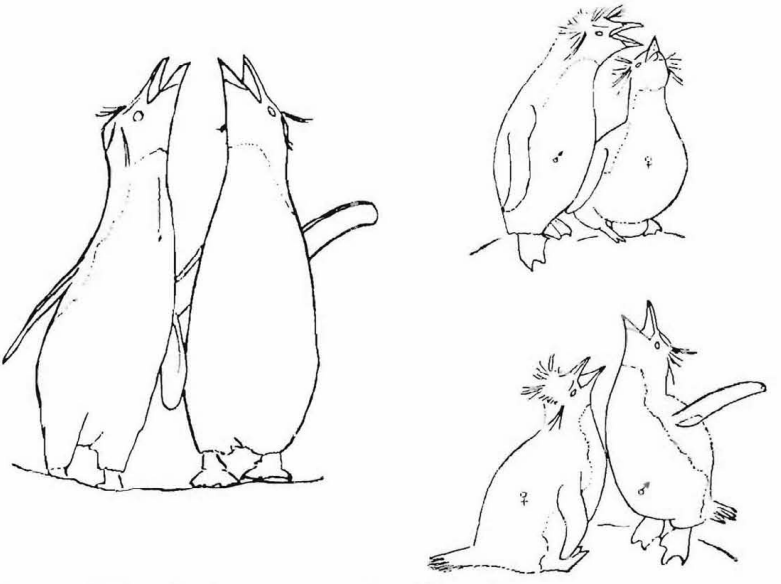

Figure 6. Left. Mutual trumpeting. Right. Mutual display.

to the sky, bills wide open, and the flippers rose and fell in time with the braying. The muscles of the chest rippled and swelled as the sounds poured forth. These were quite different from those used in mutual display, lacking the pulsating rhythm heard then, but being louder and delivered with tremendous "punch." Nor were the heads swayed or wobbled as in mutual display; they remained fairly still with the male reaching a little higher than his mate. Gradually the cries died down, the male probably changing to his special display with head wobbling, after which the whole performance subsided to throbs and silence. If the relieving bird had been off for some time this ceremony was usually repeated several times before both relaxed.

This distinctive display was rarely seen away from the nest. It occurred occasionally from the time of the females' return at the start of the season, but became more frequent during incubation. It was common in the guard stage when changes of duty took place daily.

The vertical form of this display is evidently akin to the "ecstatic" of Sladen and others, or to Richdale's "full trumpet." It appeared to be an important indication that the two birds recognized each other, and the one on the nest might bray when its mate was two yards away and had then not made a sound. The responses of pairs nearby may have been due to some infectious quality in the display but it certainly appeared that they too recognized the new arrival and greeted (or threatened) it themselves.

Trumpeting with bill forward or, less often, vertical was the normal action when single penguins returned to their nests during the crèche period; it followed the adoption of the shoulders-hunched attitude. The trumpeting was evidently the signal for the chick to leave the huddle in the expectation of a meal.

This display was twice used by immatures. A probable two-year-old displayed towards another immature and a one-year-old did so towards an adult, but was promptly driven off.

Male display.—This began with bowing, the bill being directed first at the feet and then suddenly swung back so that the crown was vertical and the beak pointed to the sky. The head was then rapidly shaken from side to side through an arc of about 30°. The flippers were sometimes held to the sides but more often were raised progressively as the display proceeded. They were not beaten in time with the calls as in trumpeting. As the head wobbled, loud, pulsating, raucous cries were given through the open bill. If the female was present she usually, but not invariably, responded with her special display, and mutual display resulted (see below).

Male display was common from the breeding males' arrival until their

departure after their first long fast. It was seen again following their return for the second incubation shift and while they guarded the chicks. Males that occupied sites but failed to find mates used the display a great deal, and it evidently had an advertising function.

Mutual display.—See Figure 6, Right. This activity began with the male bowing and throbbing and then swinging into the special action described in the previous paragraph. The female's response, if she responded at all, was to bow and perhaps to quiver. When the male swung up his head she rose to face him and, calling with her bill slightly open, she reached towards his head or neck. Her body heaved as she called but there were no violent muscle contractions, as in trumpeting. Nor was her head wobbled about as was that of her mate, her bill being kept more horizontal. Her flippers were seldom raised. Incubating females generally behaved similarly but most remained seated.

While the male's performance was often seen as a solo, that of the female was used only in response to male display or, occasionally, to a male's vertical trumpeting. Mutual display is figured by Falla (1937: 93), the male being the rear bird.

Coition.—The preliminaries to coition were similar to those in *Pygoscelis* (Roberts, 1940: 209) and *Eudyptula* (Warham, 1958b: 611) and are preceded by what Richdale terms the "arms act." The male crowded up to his mate, nibbled her nape with his bill, and flicked his flippers against her back. If receptive she then subsided and he mounted. She remained quiet, her head upraised, while with quick, jerky movements, he nibbled around her cheeks and crown. She might stretch her flippers on either side to touch the ground. His downturned flippers continued to drum her flanks as he trod with his feet, his tail swishing from side to side while he gradually edged backwards and depressed his tail so that the cloacas were opposed as she tilted her tail upward. Just before contact the female's cloaca was everted. The male now kept quite still during the climax, when his flippers propped him in place and the female's beak was turned into his neck. After about two seconds the male slid off and the female's cloaca was inverted. He remained motionless immediately after his descent, holding the shoulders-hunched attitude; she too kept quite still except for pulsations around the cloaca. Then both started to preen, shook their heads, and relaxed.

Most instances of apparently effective coition were seen between 2 and 5 November, and on 17 November it was noted that no matings had been seen for several days. Subsequent occasions, while often appearing complete, were doubtless ineffective and, where the participants were identified, they were failed breeders or non-breeders. Thus the birds of a pair at nest C that lost its eggs about 14 December were seen in

coition on 28 December. Copulation was not seen between birds with eggs or chicks and occurred only at the nest. Either sex solicited, the female by squatting or the male by beating his mate with a flipper, but after the peak period the males were the most active. Many fruitless attempts were seen when males solicited but the females failed to respond.

Birds VB (female) and WE lost their eggs about 7 December but were seen copulating seven days later, and on 28 December they did this three times. On each occasion the female was uppermost. These were the only instances of reversed coition seen and, although the sexes were clear from the male display used by WE, both were later collected. On dissection it was found that WE had only one testis, the left, which measured about 15.9 × 7.2 mm. The ovary of the female was slightly enlarged. These two birds are preserved as skins in the National Museum, Melbourne (No. 5652 male; No. 5653 female). Previous instances of reversed coition in penguins are given by Roberts (1940: 208) for the Gentoo (*Pygoscelis papua*) and by Falla (1937: 77) for the Adélie.

Coition or attempted coition was always between fully crested birds, except on 4 February 1961, when a short-crested Rockhopper was seen to pat an older bird ineffectively with its flippers in the usual invitation to mating.

Displays and Activities of a Threatening Nature

Mild threat.—This was shown when one penguin reached towards another, turned its head to one side and bobbed it up and down. The flippers were often raised ready for use and a series of short cries was given. This was the response when a strange bird walked through the rookery or when a human entered. Birds or boots that came within range were pecked fiercely or struck with the flippers.

Severe threat.—This consisted of birds jabbing their opened bills towards each other and making harsh cries. Beaks sometimes became interlocked and one of the disputants might even be pulled off its nest.

Fighting.—The penguins grappled together until one had its rival by the nape and belabored it with a flipper. Very aggressive males clung to their opponents when they fled and followed them through the colony, oblivious to the pecks they both collected from angry birds into which they blundered.

In all threat activities the males were the more vigorous. Threats were directed at any moving object close to the bird involved. Their mates appeared to be exempt through individual recognition and the resulting trumpeting greeting. Much bickering took place between breeders in the pre-egg stage and shortly after laying, when both sexes were present and the colony was crowded. Later, with immatures and non-breeders

about, an hierarchical system was established in which the breeding males dominated all the others, the non-breeding males dominated the rest, short-crested birds dominated the yearlings, and the last dominated the chicks.

Attitudes Suggesting Nervousness

The slender walk.—When a Rockhopper had to move through a mob of penguins it employed a special attitude apparently intended to shield it from attack. The body was erect but the head was rather bowed, with the bill pointing down at about 45°, the feathers sleeked, and the flippers held forward as in the shoulders-hunched attitude. Such birds hurried through places where the throng was thick and paused where there was more space. They then lifted their heads and jerked them rapidly from side to side as if trying to get their bearings.

The slender walk suggested nervousness, as the birds seldom retaliated to pecking, but it did not protect them entirely from attack if they came too near to an occupied nest. When hemmed in by others, the travellers stretched as high as possible and pushed through in an effort to get out of the area without injury. They appeared to be concerned to keep their eyes out of beak range. The attitude was rather similar to the shoulders-hunched posture seen at nest relief, into which it merged when the nest was gained.

The submissive posture.—The sitting bird flattened onto the nest, drew in its head, and kept still while an attacker pecked it and beat it with a flipper. Such behavior was seldom seen and only as a reaction by incubating females to attack by strange males. Some attacks seemed to be due to a male's misidentification of his nest site. The posture had obvious value in that the eggs or chicks were protected by the female mantling over them; had she retaliated the eggs might well have been broken or the chick injured. Furthermore, the submission of her nape to the aggressor may have helped to inhibit pecking as it does in the Australian Gannet (*Sula serrator*) and other birds (Warham, 1958a: 349). Two instances may be detailed:

> On 12 November 1960 an intruder entered the colony and, using the slender walk, approached nest R where a lone female was incubating. The newcomer began belaboring the female. She pulled in her head, flattened her body, and tucked her bill into the nest. The intruder gave the male display several times and then half-preened and half-pecked the female's head. She did not move. Soon another banded penguin appeared, wet from the sea. This was the correct male for nest R and he immediately dived at the intruder, ejected him, and then broke into loud trumpetings in which his mate joined.
>
> On another occasion the submissive female was apparently on the wrong nest. Her attacker was joined by a female and both combined in mutual display. The squatting bird then got up and moved off, after which the new female sat down.

Wing shivering.—It is often thought that penguins are unaffected by the proximity of people. That this belief is wrong is suggested by the nervous way in which the Rockhoppers nearest the human observer shivered their flippers through a small amplitude, like an insect warming up its muscle engine in preparation for flight. Comparable behavior is seen in other penguins and in the Procellariiformes.

Unclassified Attitudes and Actions

The head shake.—All penguins of the genus *Eudyptes* punctuate their activities with rapid side-to-side shakes of their heads so that these appear blurred. Anything adhering to the bill, such as nesting material, droplets of excretion from the nasal glands, etc., is shot to one side. Head-shaking in the Rockhopper invariably follows any period of activity, and R. Carrick has suggested that it serves as a "full-stop," marking a return to rest.

The squeal.—Occasionally a sudden and penetrating cry, sustained for several seconds, was heard in the colonies. No movements accompanied the sound which seemed to be given through a closed bill. Rarely was the bird responsible identified, although the call was heard many times and at close quarters throughout the breeding season. The squeal may have arisen from fear because, while incubating, one bird cried out as a skua flew very low, others repeated the cry, and a strange hush fell over the colony. It was rather like a "dread" among terns. Similarly, a one-year-old was seen to squeal on sighting the approach of the owner of the nest upon which the younger bird was standing. A third instance was noted when one of a party of molted adults squealed several times as they teetered on the rocks, hesitating before plunging into the water.

Individual recognition may have been involved when on 8 February 1961 a male on its nest squealed loudly just before his mate reached him, then broke into the usual trumpets of greeting.

The Molt

After their chicks departed, the adults were at sea for about five weeks. They reappeared from 25 March onwards, much heavier than on leaving, weighing 3.2 to 4.1 kg, with an average of 3.5 kg from seven determinations. The normal weight of a mixed sample of both sexes was 2.6 kg. Some 7 to 10 days elapsed before the first feather fell, and the plumage was now dull brown, the birds getting very obese as the new feathers pushed out the old. Feathers fell first from the tail, and 14 to 22 days elapsed, with an average of 17 days from 28 records, before the last feather was shed. The penguins fasted throughout this period. The new plumage was blue-gray in color and the birds were very sleek. Their

weights now averaged about 2.3 kg from five determinations, a fall of some 1.2 kg to slightly below the normal figure.

Molting birds were subdued, but the shoulders-hunched attitude, the quiver, some trumpeting, mutual preening, and even stone-carrying and nest-making were occasionally seen. No attempts at coition were noted, as happens with *Eudyptula minor* (Warham, 1958b: 615) and *Eudyptes pachyrhynchus* (Richdale, 1941: 35, 39). During the two to nine days (average 5.5 days from 11 records) from the end of the molt to the birds' departures for the winter, some descended to bathe in rock pools. A few still in molt did the same.

In 1961 J. McNally found that 17 of 22 successful breeders molted on their nests. Of four successful pairs only one bird each reappeared. These either molted alone or formed attachments with neighbors. A lone female, VL, from nest P molted with male VN from R whose own mate failed to appear, and these two bred together in the 1961–62 season. Unsuccessful breeders also molted together, but again, with four pairs, only one bird was resighted.

The members of any pair seldom arrived together and unless both finished at the same time they returned to sea independently. The pair, nest Y, provided an extreme instance: the female molted at her nest with a new bird and left on 28 April 1961 two days before her proper mate reached the rookery to start molting on 5 May. He was the last bird on the colony that season.

The data are insufficient to determine whether failed breeders molt before successful ones. Four failed breeders finished a few days before most of the successful birds, two finished concurrently with them, and the mateless male WB also molted four days in advance of the successful breeders.

Tenacity to Site and to Mate

At least 13 pairs bred in the 1961–62 season with the same mates and at the same places as in the previous year. Six birds bred on their previous sites with new mates, their old partners not having reappeared. Five others had new mates and bred at new sites. These included two penguins that were mated in 1959–60, took new partners in the following year but reverted to their previous alliance in 1961–62. Another pair did not remate in 1961–62. Instead, each took a new partner and nested independently. Not less than 11 of the banded males bred at the same sites in 1959, 1960, and 1961. There are also four records of birds banded in 1957 by M. P. Hines that were breeding at the same nest-marker in the 1960–61 season and two records of birds that had shifted their nests a few yards. Pair XA and XI, banded together in April, 1957, molted

together in March, 1960, and reared a chick in 1960–61. Although their original nest-marker was missing they were evidently breeding very near to their site at banding four years before.

These records suggest that breeding Rockhopper Penguins continue to be reunited for successive seasons if both members of a pair reappear at the rookery and that they reoccupy the same nest sites as they previously held. When one bird fails to return, the survivor either acquires a new partner and breeds at its customary site or shifts to a new one. In the event of a pair failing to return, the nest is taken over by new birds and no blank spaces are left in the centers of the colonies. As shown above, while a male may acquire another partner at the start of a season, she is quickly discarded in favor of the old one when the latter returns.

Enemies and Mortality

Detailed figures for breeding success were not obtained. Of the 30 pairs at the study colony, 28 laid eggs in 1960 and 22 produced chicks to the crèche stage. Causes of failure were: no eggs laid, or eggs lost before being seen, 2; egg incubated but infertile, 1; egg lost during female's first shift, 2; egg lost during male's first shift, 1; egg or chick lost at hatching, 1; chick died in guard stage, 1.

These findings support the impression gained at larger colonies that most losses occurred during egg-laying and incubation. While it was usual for the small egg to be ejected, some birds also ejected the large one. Most of such eggs were taken by skuas and by Wekas (*Gallirallus australis*). Rats were not known to be responsible for any losses.

During January and February occasional Rockhopper Penguins were found bearing gashes on their breasts. These were apparently victims of the fur seals (*Arctocephalus forsteri*) now recolonizing the island and most plentiful in these months.

Acknowledgments

I am grateful to members of ANARE who helped in this work and particularly to M. Simon and J. McNally of the 1960–61 and 1961–62 parties, respectively, who made regular observations during my absence on other duties. Mr. McNally continued observations after my return to Australia, and some of his findings have been incorporated in this paper. Dr. R. Carrick and Mr. S. Davies kindly read the preliminary draft and suggested many improvements.

Summary

1. A study of the Rockhopper Penguin (*Eudyptes chrysocome*) in 1960 and 1961 was based mainly on observations of banded breeders. The birds were sexed on bill differences and on behavior.

2. Breeding males were the first to return to the island after spending the winter at sea. They went to the places where they had previously

bred and molted and were joined about 6 days later by their previous mates.

3. After a week, during which both sexes changed over frequently on the eggs, the females took the first shift of about 14 days. The males then incubated for about 10 days and the females returned a few days before the hatch. The incubation period was 34 days.

4. The males did not return to sea when the females reappeared but brooded or guarded the chicks for about 26 days, after which the chicks deserted the nests and entered a crèche. During the guard stage only the females fed the young, returning each evening for this purpose.

5. In the crèche stage both parents went to sea by day and fed the chick in the afternoon or at night. They fed only their own young, near or at the nest site. Chicks left when about 70 days old and did not return to the island until the following season.

6. Non-breeders and failed breeders dominated the rookery during the crèche stage, the males interfering with females trying to feed their chicks.

7. Immatures molted in late January and most had left by the end of February. Breeding birds molted in mid-April after about 28 days at sea. They had then been ashore 31 days, 17 days of which were occupied in shedding the old feathers.

8. Rockhopper Penguins had many dramatic displays which are described. Males had a display not used by females and of value in sexing the birds.

9. Reversed coition was noted with one pair whose sexes were confirmed by dissection.

10. Rockhopper Penguins exhibited a strong tendency to return to their nest sites and mates from year to year. Several nested in 1960–61 at the same sites as those they occupied four years before.

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CHAPTER 3.

BREEDING SEASONS AND SEXUAL DIMORPHISM IN ROCKHOPPER PENGUINS.

BREEDING SEASONS AND SEXUAL DIMORPHISM IN ROCKHOPPER PENGUINS

JOHN WARHAM

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BREEDING SEASONS AND SEXUAL DIMORPHISM IN ROCKHOPPER PENGUINS[1]

JOHN WARHAM

VISITS to Campbell Island (52° 33′ S, 169° 09′ E) from 8 to 26 January 1969 and to Antipodes Island (49° 40′ S, 178° 50′ E) from 28 January to 12 March 1969 permit some comparisons between two breeding populations of the Rockhopper Penguin (*Eudyptes chrysocome*) and supplement data gathered at Macquarie Island between 1959 and 1961 (Warham, 1963). The present paper forms part of a series to deal with aspects of the breeding biology of all the *Eudyptes* penguins.

Bailey and Sorensen (1962) describe the distribution and breeding of the Rockhopper Penguin at Campbell Island, which supports many more Rockhoppers than other penguin species. Small numbers of Erect-crested Penguins (*E. sclateri*) also nest there, and Royal Penguins (*E. chrysolophus schlegeli*) are not rare though not known to breed. The Yellow-eyed Penguin (*Megadyptes antipodes*) is the most plentiful penguin after the Rockhopper, but breeds among thick vegetation well away from the latter bird. At Antipodes Island Rockhoppers share breeding beaches and coastal slopes with large numbers of *E. sclateri*. The latter generally occupy the lower and reasonably flat ground above high water while the Rockhoppers nest higher up, often on steep slopes or within shallow caves. At this island the two species appear to occupy nesting niches equivalent to those Royals and Rockhoppers take up at Macquarie Island where, when the two species are contiguous, the latter again lay higher up among talus debris consolidated by soil, or among tussock grasses.

At Campbell Island the data were collected from live birds at a small colony in Rocky Bay below Mt. Dumas and at a larger one at Penguin Bay. At Antipodes Island Rockhoppers occur mainly on the east and south coasts; the data here were gathered at two colonies in the vicinity of the expedition base at Reef Point on the eastern side of the island. Colony locations with indications of size are being mapped and will appear with a general account of Antipodes Island birds (Warham and Bell, MS.).

The Expedition was assisted by a grant from the Trans-Antarctic Expedition Research Fund and thanks are also due to the Royal New Zealand Navy for providing transport, to R. Stanley for help in the field, and to K. W. Duncan for advice on statistics.

[1] University of Canterbury Antipodes Island Expedition 1969, Paper No. 4.

The Timing of the Breeding Cycle

Rockhopper chicks on Antipodes Island in 1969 were at a more advanced stage of development than were those on Macquarie Island at the same dates in 1960 and 1961. Thus on 5 February 1969 many were completely feathered and by 9 February some had already left for the sea. The main chick exodus occurred within the next 7 days and all the chicks had gone from the Reef Point colonies by 20 February. Indeed, after about 15 February most colonies were almost deserted for the yearlings had molted and left, although at some of the bigger colonies on the south coast a sprinkling of birds remained, mostly in molt. These probably included a number of failed breeders, but a last check of the nesting areas at Reef Point and at Alert Bay 1 mile farther south on 10 March showed these colonies empty and the breeding birds still at sea feeding in anticipation of their annual molt.

Comparing these data with those from Macquarie Island shows that the season at Antipodes Island is about 12 days earlier. This would set the peak of egg-laying (the date at which 50 per cent of the pairs have laid one egg and 50 per cent have laid two) at approximately 1 November, as this peak is around 13 November at Macquarie Island. This estimate is confirmed by E. G. Turbott who made several landings at Antipodes Island between 4 and 10 November 1950. He reports (pers. comm.) that during this period most birds were sitting on two eggs, the larger one being clean and thus new-laid.

Compared with Macquarie Island chicks, those at Campbell Island were also somewhat advanced but less so than the Antipodes Island birds. Thus 47 chicks on 10 January had a mean weight with one standard deviation of 1312 ± 272 g as compared with a weight of approximately 600 g at Macquarie Island for the same date. Similarly 41 chicks from the same group weighed 1577 ± 339 g on 17 January compared with a mean for that date of about 1150 g at Macquarie (Warham, 1963, Figure 3). These data, in conjunction with the dates listed by Bailey and Sorensen for various episodes of the breeding cycle, indicate a peak of egg-laying at Campbell Island about 4 days earlier than that at Macquarie, i.e. about 9 November.

Many years ago Murphy (1936) drew attention to the wide variations in the breeding seasons of the different populations of this penguin and noted that these were correlated with latitude. The breeding islands lie on both sides of the Antarctic Convergence and between 36° and 53° S. The data available to Murphy were rather fragmentary but later work enables this variation to be examined more precisely.

Breeding data are given by Paulian (1953) for Amsterdam Island and Kerguelen; by Elliott (1957) for Tristan da Cunha; by Swales

(1965) for Gough Island; by Murphy (1936), Pettingill (1960), and Strange (1965) for the Falklands; by Murphy (1936) for Ilde fonso Island, Cape Horn; by Downes et al. (1959) for Heard Island; and by Rand (1954) and La Grange (1963) for Marion Island.

I have either taken the dates for the peaks of egg-laying from these authorities or, where they do not give them, have calculated the dates by assuming that the lengths of the various stages of the breeding cycles do not vary appreciably from those at Macquarie Island as detailed in my previous paper and also that the breeding dates have not altered appreciably in recent years. At Macquarie Island for instance the timing of the season today seems to be the same as it was 50 years ago.

When these dates are plotted against latitude a rough correlation is revealed, but with Heard Island and Kerguelen lying well away from the trend line; the birds breed later here than at other colonies in similar latitudes. Plotting the peak of egg-laying dates against mean annual sea temperature produces the linear relationship shown in Figure 1. These temperatures have been taken from Stonehouse (1967) who derived them from the isotherm charts for February, May, August, and November rather than from actual determinations at sea near the islands, although they agree with data from other sources where these are available.

The egg-laying data for most of these islands are still imprecise and errors of several days may be involved owing to the necessity of deducing egg-laying peaks from hatching dates, for instance. The information for the Falklands illustrates this. Murphy (1936: 423) stated that the first eggs are laid in the last days of October, that within 3 days a colony will be well sprinkled with them, and that before a week has passed there will be at least one egg in practically every nest. From this I estimate a peak of laying around 6 November as at Macquarie most eggs are laid over a 10-day period. Murphy's figures suggest therefore that laying at the Falklands is about a week earlier than at Macquarie, as plotted in Figure 1. At Beauchêne Island, about 60 miles south of the main group, Strange (1965) found the birds with young only a few days old on 2 to 6 December, 1964, perhaps as much as a fortnight in advance of those at Macquarie. Yet Pettingill (1960) working at New Island, estimated that on 29 December 80 per cent of the birds had chicks varying from day of hatching to 1 week old, 10 per cent chicks older than that, and 10 per cent with eggs. Thus hatching there seems to have been at a peak around 25 December which, allowing for an incubation period of 33 days and 4 days between first and second eggs would give a peak of egg-laying of about 20 November considerably later than at Macquarie Island.

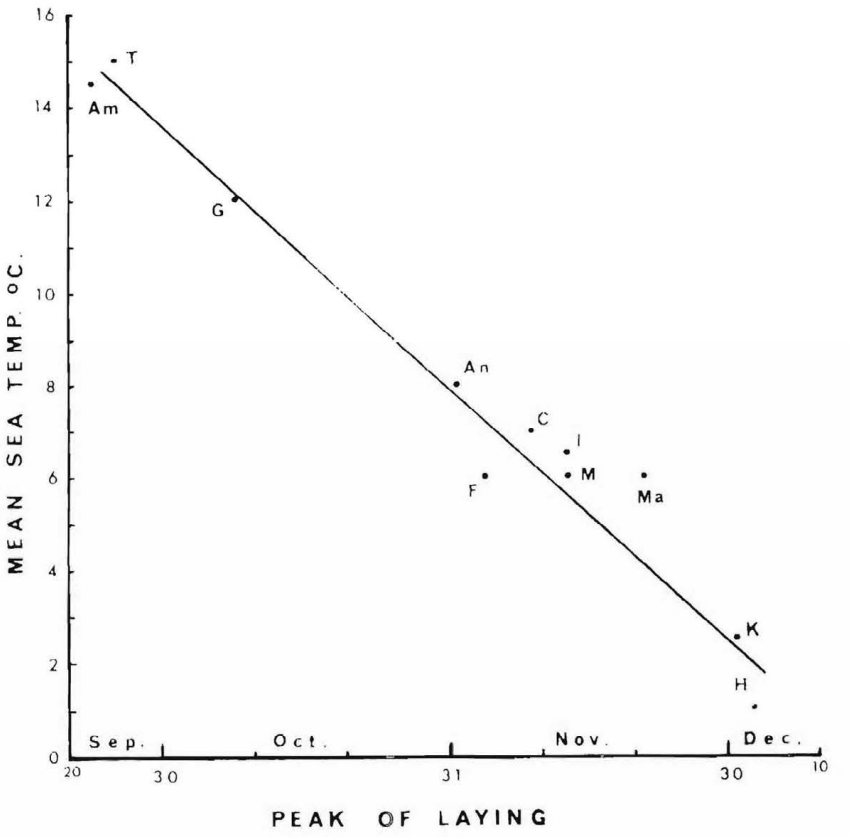

Figure 1. The relationship between the date of peak of egg laying and mean annual sea temperature. Am, Amsterdam Island; An, Antipodes Island; C, Campbell Island; F, Falklands Islands; G, Gough Island; H, Heard Island; I, Ilde fonso Island; K, Kerguelen; M, Macquarie Island; Ma, Marion Island; T, Tristan da Cunha.

Possibly Pettingill's chicks were older than he thought, but he also drew attention to differences in the ages of chicks in different sections of a colony that was broken up into discrete parts by headlands. Hence laying dates may perhaps vary even on the same island from one colony to another. A variation in the development of chicks between colonies on the same breeding station has also been noted in *Eudyptes chrysolophus* (Downes et al., 1959: 13; Warham, 1971).

Despite such inconsistencies it is clear that the peaks of laying differ by over 3½ months between islands at the extremes of the species range, and Figure 1 suggests that the dates of laying advance about 10 days for each degree centigrade rise in mean sea temperature.

Such a correlation is not surprising for a bird spending most of its life in the sea, but whether the link is a direct one and temperature, for example, influences gonad resurgence via sensory input to the hypothalamus, or is indirect, perhaps by way of the food supply, can only be conjectured. We know little of the food spectra of the birds at various breeding stations nor of their wintering areas at sea. Stonehouse (1967) discusses the physical factors that may affect penguins at sea. Being highly specialized animals, not least in their temperature regulatory mechanisms, each species may well be imprisoned within a narrow span of isotherms for which it is physiologically adjusted—to use his phraseology. Swales (1965) also suggests that small differences from year to year in penguin landing dates at Gough Island may be related to differences in the position of the subtropical convergence and hence of sea temperature.

According to Stonehouse's figures the mean sea temperature at South Georgia resembles that at Heard Island, although at South Georgia the extremes of sea temperatures are greater and these may have a bearing on the absence of the Rockhopper from South Georgia as a breeding species (Carrick and Ingham, 1967).

Marion Island seems to show a considerable divergence from the correlation with sea temperature. Judging from the information given by Rand (1954) egg-laying is at a peak there about 10 days later than it is at Macquarie Island although both places have similar mean sea temperatures. His data are supported by those of La Grange (1963) whose figures suggest a peak of laying around 21 November. That the birds should lay late here is particularly anomolous as Stonehouse's data show air temperatures at Marion are appreciably higher than at Macquarie Island.

While the bird's late arrival at Kerguelen and Heard Island may well be influenced by the cold local conditions induced by their extensive ice sheets, there appear to be no physical barriers preventing earlier landings, and the congeneric Macaronis (*E. c. chrysolophus*) arrive about 14 days before the smaller Rockhoppers do.

Interspecific competition with larger Eudyptids could also be a factor affecting laying dates, for wherever two Eudyptids breed abundantly on the same island, it is the smaller Rockhopper that arrives and lays last. At Amsterdam, Tristan da Cunha, Ilde fonso, and Gough Islands there are no other Eudyptids, at the Falklands only a few Macaronis, and at Campbell Island only a few Erect-crested Penguins. Large numbers of *sclateri* breed at Antipodes Island and *chrysolophus* at Macquarie, Marion, Kerguelen, and Heard Islands. At such places there seems to be little overt competition between the two species except possibly for

nesting sites, although some fighting does occur. On the other hand, competition may be important at sea. As all three species seem to feed their chicks almost daily, the feeding range during chick rearing must be limited. Competition seems quite likely to occur then and perhaps at other times during the year, and the later laying of the Rockhopper could have evolved in response to his kind of competitive pressure.

If such an effect exists it is not immediately apparent from the data. For example, laying at Campbell and Ilde fonso Islands, where Rockhoppers have little or no Eudyptid competitors, is not particularly early. Furthermore where the Rockhopper breeds in company with a larger Eudyptid, the feeding periods for the chicks of the two species overlap for about a month despite the later laying of the smaller species. Competition would be reduced, of course, if the two species took different sized prey, as they may well do judging from interspecific differences in bill size.

The later laying of the Rockhopper could be due simply to later arrival in consequence of its smaller size and a reduced capacity for heat retention in comparison with he larger species.

The role of sea temperature in he timing of the laying season is thus by no means clear, and this discussion draws attention to the need for more precise information on the breeding seasons and food preferences at the different islands.

Sexual Dimorphism

It has long been known that adult male Rockhoppers are bigger and heavier than adult females, and Murphy (1936) gave comparative dimensions based on small samples. During my previous studies of this penguin the reality of the difference in bill size was repeatedly confirmed because the birds could be sexed at copulation, by a sex-specific display and other behavior, and occasionally by dissection, but no birds were measured. This sex-specific display was termed the "male display" in my earlier paper. In it the bird swings its head back until the crown is vertical and then shakes its head rapidly through a narrow arc while calling loudly. In my experience this action is used exclusively by male Rockhoppers, these same birds being the ones that were uppermost during copulation, the most aggressive partners in defense of the nest and the ones that mantled over the chicks during the guard stage (Warham, 1963: 248).

Sexual dimorphism appears also to extend to tarsal and midtoe with claw lengths, but in order to make the best use of the limited time available in the present study it was decided to concentrate on body weights and on the dimensions of beaks and flippers in attempting to

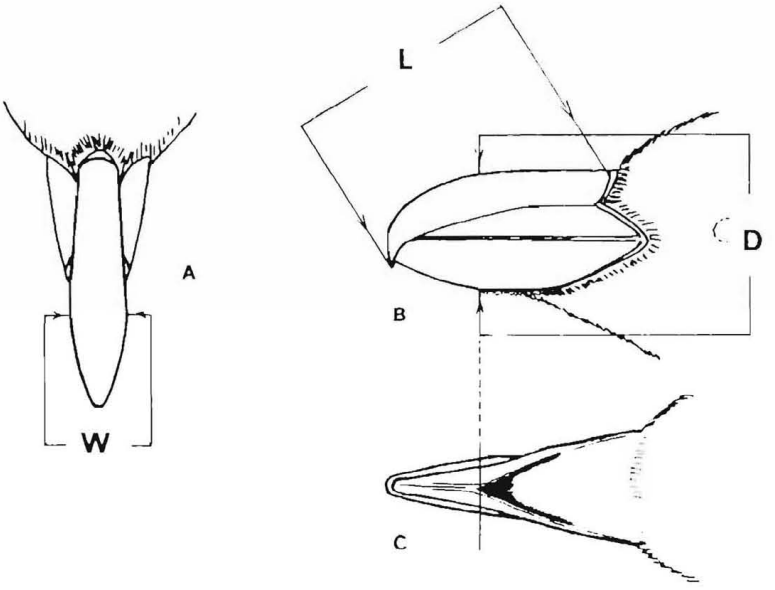

Figure 2. Methods used for bill measurements; A, culmen width (W); B, culmen length (L) and bill depth (D); C, underside of bill showing point just proximal to diverging mandibular rami at which depth was measured.

evaluate the differences and to ascertain whether they could be detected in younger birds.

The length of the flipper was determined by pressing it along a rule butting against the body at the axilla. The bill was measured with vernier calipers taking the length of exposed culmen (L), the maximum width of the culminicorn (W), and the depth of the bill (D) taken at a point just proximal to the tip of the triangular inter-ramal feather patch as shown in Figure 2. A beak shape index was then calculated as

$$\frac{LWD}{10}$$

in mm. This gives a measure of the gross size of the bill. Weights were taken using a spring balance accurate to ± 25 g.

Data were collected from 10 pairs of live adults at Campbell Island on 17 January, from a further 59 adults at Campbell Island at that date, and from 94 adults at Antipodes Island on 9 February. Yearlings measured included 24 at Campbell Island on 13 and 17 January and 32 at Antipodes Island between 9 and 14 February. Finally 72 chicks were measured at Antipodes Island between 9 and 12 February.

TABLE 1

MEASUREMENTS OF TEN PAIRS OF ROCKHOPPER PENGUINS AT CAMPBELL ISLAND ON 17 JANUARY 1969[1]

	♂♂	♀♀	$\frac{♂♂}{♀♀} \times 100$
Bill length mm	46.4 ± 1.37 (2.95)	41.1 ± 2.05 (4.98)	113
Culmen width mm	10.6 ± 0.23 (2.17)	9.2 ± 0.25 (2.71)	115
Bill depth mm	20.7 ± 1.07 (5.17)	17.8 ± 0.67 (3.76)	116
Beak shape index	1017 ± 73 (7.18)	670 ± 64 (9.55)	152
Weight g	2757 ± 274 (9.94)	2395 ± 52 (2.17)	115
Flipper length mm	167 ± 4.4 (2.63)	167 ± 3.4 (2.04)	100

[1] Mean, one standard deviation (coefficient of variation).

The 10 pairs measured on 17 January either had chicks or were standing together at nests. In three instances the smaller bird was wet, for the guard stage of the chicks was ending and there was a fairly steady traffic of wet birds entering the colony to feed chicks and of dry ones leaving it, but few pairs to be seen with chicks. One bird of each pair measured looked heavier billed and was the more aggressive when captured. Some of these also gave the male display on reaching their nests after release. The dimensions of these paired birds are summarized in Table 1.

With the exception of flipper length, the male values for each parameter differed significantly ($P < 0.001$) from those for the females. In no dimension except flipper length was any female larger than her mate, the ranges also being mostly nonoverlapping. It might have been expected that some females would weigh more than their mates with the females going to sea daily at this date, whereas some of the males had probably only just been released from their long fasts during their guarding of the chick and thus should have been quite thin, but even in body weight the dimorphism was complete. It will be noted, however, that the males' weights were more variable, mainly due to three that weighed 3000, 3050, and 3250 g. None of these wore the dull plumage usual in birds ready to molt.

At neither island were banded birds available and it is difficult to capture pairs once chick guarding has ended. For closer examination of the size differences, data from individual birds tending chicks or believed from their behavior to be breeders had to be used. Therefore the samples of 94 Antipodes Island and 59 Campbell Island birds probably included a few prebreeders (birds in adult plumage not yet mature enough to breed) and failed breeders.

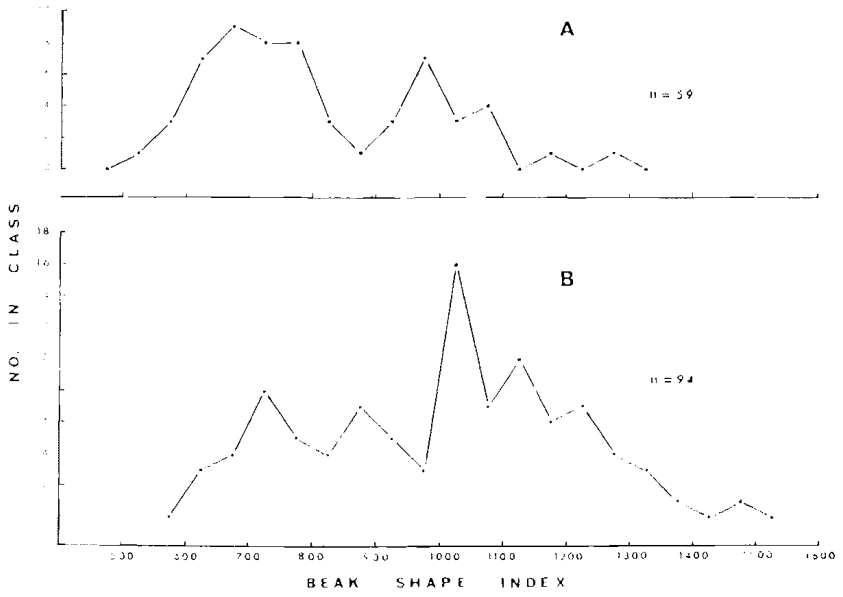

Figure 3. Distribution of adult beak shape indices, A from Campbell Island, B from Antipodes Island.

When capturing these birds it was usually impracticable to sex them by behavioral characters and none was dissected. In 11 instances measured birds were seen to give the male head shaking display. Ten of these birds were later judged to be males from their beak shape indices; the other had a value for this parameter lying in the zone of overlap.

The data from the two islands had to be handled separately as the birds' dimensions showed significant differences, Antipodes Island birds being bigger billed but lighter in weight.

Adult Beak Size

Figure 3 shows the distribution of beak shape indices in the two samples. Both polygons appear to be bimodal suggesting that two normal distributions may be involved, one for each sex, but the peaks for the two islands do not coincide. Each distribution is projected on probability paper in Figure 4.

In these graphs the points of inflexion indicate that about 43 per cent of the birds in the sample from Antipodes Island lay in the lower size class and were presumably females, whereas about 66 per cent of those in the other sample were in that category. Replotting the points that fell on either side of the inflexions on the premise that the bimodality was due to the interaction of two normal distributions, one for each sex, according to the methods of Harding (1949), produced lines CD and EF for the Campbell Island birds and GH and IJ for those

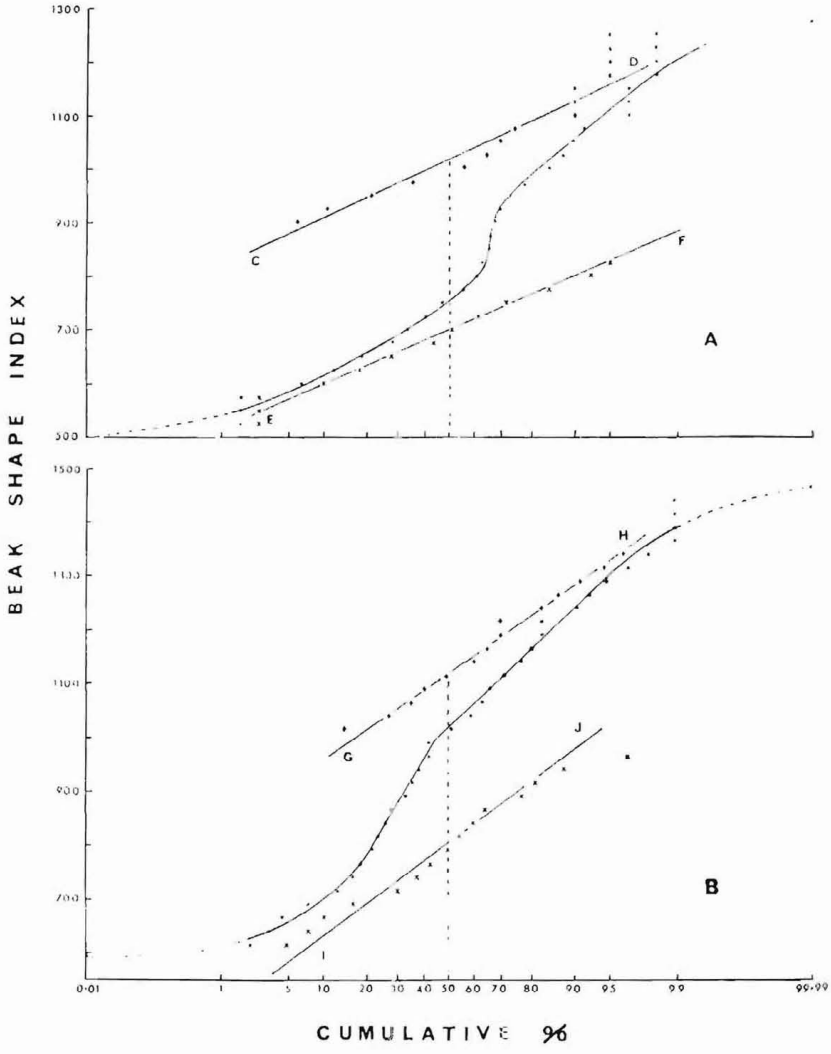

Figure 4. Polymodal frequency analysis of adult beak shape indices, A from Campbell Island, B from Antipodes Island.

for Antipodes. From these the means (50 per cent level) plus or minus one standard deviation (84.1 and 15.8 per cent levels) were read off. They are given in Table 2. In the Campbell Island sample the overlap between the sexes was quite small and at the point of inflexion includes only 2 per cent of females and 3 per cent of males whereas in the Antipodes Island sample the point of inflexion includes 8 per cent of the females and 16 per cent of the males.

TABLE 2
BEAK SHAPE INDICES FOR ADULT ROCKHOPPER PENGUINS

	Campbell Island	Antipodes Island
Females	690 ± 80 (11.6)	805 ± 135 (16.7)
Males	1010 ± 85 (8.4)	1120 120 (10.7)
$\frac{\text{Males}}{\text{Females}} \times 100$	146	139

Using the product of length, width, and depth to measure bill size tends to emphasize differences in this character and it is not surprising that the curves for beak indices separate so clearly, the differences in the means of the two size groups being highly significant ($P < 0.001$). However when the distributions of the three components were examined separately by the same graphic technique, the bimodalities were less clear-cut and the points of steepest slope that mark the transition from one distribution to the other did not always lie close to those found when the beak index data were analyzed.

Beak widths segregated clearly, depths less so but sufficiently for analysis, whereas the tails of the curves for beak length evidently overlapped considerably, requiring larger samples for the separation of the sexes on this character. Unfortunately it was not possible to sex all these birds on anything but beak characters, and so to get a better estimate of bill lengths the examination was restricted to those birds that could be sexed confidently on beak shape indices. Antipodes Island birds were judged to be females when their beak shape indices were less than 940 (n = 34), males where these were greater than 1020 (n = 49); Campbell Island birds with indices less than 780 were taken to be females (n = 33), those having these greater than 870 to be males (n = 20). From these reduced samples, means and standard deviations were derived using standard formula.

Table 3 shows the results of combining the information for beak depths and widths derived from the graphical analyses using all the data, with those from beak lengths using the more restricted data. The shape indices calculated from the separate estimates of the three components agree well with the indices derived directly from Figure 4. The Campbell Island figures also agree satisfactorily with the small samples analyzed in Table 1. Bill lengths may be compared with the figures given by Westerskov (1960) for freshly killed birds from Rocky Bay, Campbell Island: means for 6 males and 13 females were 44.1 and 40.3 mm respectively.

Table 3 thus gives a best estimate of the mean values for the beak components in the two samples and the differences between the means for the sexes at an island and between islands are all significant with $P < 0.001$ in each instance. As some of the variability in the samples was eliminated by discarding intermediate values in selecting the data, the values for beak length will be slightly below the true mean for the females and slightly high for the males.

This analysis shows that the Campbell Island birds were clearly smaller billed than those at Antipodes, but the degree of difference between the sexes for each bill component was very constant, the values for the males being between 11 and 14 per cent higher in all instances.

TABLE 3

DIMENSIONS OF BILL COMPONENTS IN MM AND BEAK SHAPE INDICES FOR ADULT ROCKHOPPERS

	Length	Width	Depth	Beak index
Campbell Island				
33 females	40.5 ± 1.91 (4.7)	9.2 ± 0.4 (4.9)	18.0 ± 0.7 (3.9)	670
20 males	46.3 ± 1.92 (4.1)	10.4 ± 0.4 (4.3)	20.3 ± 0.8 (3.9)	977
$\frac{\text{Males}}{\text{Females}} \times 100$	114	113	113	146
Antipodes Island				
34 females	41.8 ± 1.86 (4.5)	9.7 ± 0.6 (6.5)	18.8 ± 0.8 (4.3)	762
49 males	47.8 ± 2.32 (4.9)	10.8 ± 0.5 (4.7)	21.1 ± 1.6 (7.5)	1089
$\frac{\text{Males}}{\text{Females}} \times 100$	114	111	112	143

ADULT FLIPPER LENGTH

The raw data on flipper lengths when plotted on probability paper suggested the existence of bimodalities but with a considerable degree of overlap. Consequently analysis was restricted to data from birds sexed on their beak shape indices, the criteria being the same as those used when estimating bill lengths.

In the sample from Antipodes Island, 50 birds were judged to be males, 34 to be females. Their flipper lengths were found to be distributed almost normally around means of 167.8 ± 3.75 mm for the males and 162.8 ± 3.98 mm for the females. These values are significantly different, $P < 0.001$.

Of the Campbell Island birds 33 were judged to be females (beak shape indices <780) and 20 to be males (beak shape indices >870). The data for the males were not normally distributed and had a mathematical mean of 168 mm. Those for the females approached a normal distribution with a mean of 164.6 ± 3.6 mm, a figure hardly different ($0.5 > P < 0.01$) from that of the similarly sized sample from Antipodes Island. The Campbell Island figures may be compared with the means given by Westerskov (1960) for 6 males and 13 females of 164.3 and 161.8 mm respectively.

These data suggest that the sexual dimorphism also extends to flipper lengths, those of the males being longer, but with a considerable degree of overlap, some adult females having flippers as long as or longer than some adult males. Those of the Antipodes Island males averaged only 3 per cent longer than those of the females.

ADULT BODY WEIGHTS

Figure 5 gives the distribution of the body weights of the birds in the two samples. Both graphs show evidence of two modes, but these do not coincide with those seen in Figure 4 where the beak shape indices for the same birds were plotted. Whereas the latter indicate male to female ratios of 57:43 for the Antipodes and 34:66 for the Campbell Islands samples, the weights segregate at 35:65 and 16:84 ratios when analyzed graphically. Evidently the weight distributions at the time of sampling were only partly related to the sexes of the birds. This was further

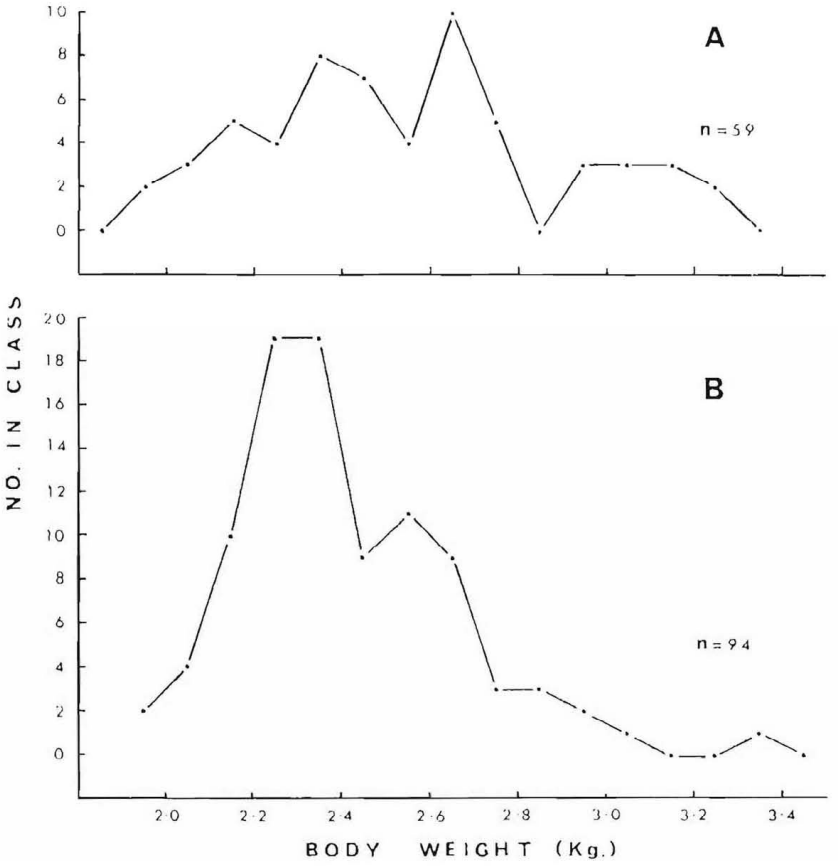

Figure 5. Distribution of adult body weights: A, Campbell Island; B, Antipodes Island.

shown by the relatively low correlation between body weight and beak shape index; $r = +0.321$, $P < 0.01$ and $+0.307$, $P < 0.02$ for the Antipodes and Campbell Island samples respectively.

Penguin weights vary greatly during the time the birds are ashore as the breeding cycle involves both sexes in long fasts. As has already been pointed out the females might have been expected to be in better condition late in the breeding cycle than their mates. Nevertheless when the weights were reexamined using information only from birds sexed on bill size, the males in both samples were found to be significantly heavier than the females ($P < 0.001$). The data are given in Table 4.

Despite the larger bills of the birds from Antipodes Island they prove to be lighter than those from Campbell Island ($P < 0.001$ for the males, $P < 0.01$ for the females). However to compare body weights from two breeding populations, one should either take data gathered at the same stage of the breeding cycle or

TABLE 4

BODY WEIGHTS (G) OF ADULT ROCKHOPPER PENGUINS SEXED ON BEAK SHAPE INDEX

Campbell Island	33 females	2570 ± 280 (11.8)
	20 males	2720 ± 250 (9.2)
	$\frac{\text{Males}}{\text{Females}} \times 100$	115
Antipodes Island	33 females	2225 ± 140 (6.3)
	49 males	2425 ± 230 (9.5)
	$\frac{\text{Males}}{\text{Females}} \times 100$	109

use fat-free weights to allow for the gain and loss of subdermal fat. The Antipodes Island birds measured on 9 February are being compared with others measured 23 days before and, as the Campbell Island penguins lay about 8 days later than those at Antipodes, the differences are aggravated. The low values for the Antipodes Island birds may reflect the wear-and-tear of chick rearing as the figures were collected very late in the breeding season. The true mean values corrected for varying fat reserves for Antipodes Island birds may well be higher than that of those at Campbell Island, but the present information does not allow these means to be estimated.

YEARLINGS

Young Rockhoppers come ashore at about hatching time as 1-year-olds, and most have molted and departed by the time the chicks fledge. These yearlings are short-crested, usually rather pale on the throat, and with duller bills and eyes than those of the adults. After the molt they are similar except that their throats are now black so that they are difficult to distinguish from 2-year-olds as the latter also tend to be rather short-crested.

Table 5 summarizes data from 24 immatures measured at Campbell Island on 13 and 17 January and 32 measured at Antipodes Island between 9 and 14 February. One or two 2-year-olds may have inadvertently been included, but otherwise all were believed to be yearlings.

The data confirm subjective observations that 1-year-olds are smaller, often lighter in weight than adults at equivalent stages of the annual cycle, and smaller billed. The bills of the 24 birds of mixed sex from Campbell Island were intermediate in size between those of adult males and females but nearer those of the females. The bills of the 32 Antipodes birds were more divergent, being smaller than adults of either sex. Although the mean beak shape index for the Antipodes yearlings was greater than that for the Campbell Island ones, the reverse situation to that of the adults, the differences of the means between islands in Table 5 are not significant for any parameter except for body weight.

The sample from Campbell Island is too small for further analysis, but graphical analysis of the distribution of beak indices from the Antipodes Island birds indicates a 50:50 ratio between two groups, one having a mean beak index of 780 ± 75 and the other of 630 ± 75, which are presumed to refer to the males and females

TABLE 5
MEASUREMENTS OF YEARLING ROCKHOPPER PENGUINS

	Campbell Island	Antipodes Island
Number	24	32
Bill length mm	42.3 ± 2.3 (5.5)	41.7 ± 2.5 (6.1)
Culmen width mm	9.4 ± 0.5 (5.4)	9.2 ± 0.5 (5.5)
Bill depth mm	18.5 ± 1.3 (6.8)	18.5 ± 1.1 (5.7)
Beak shape index	739 ± 99 (13.4)	711 ± 99 (13.9)
Weight g	3132 ± 337 (10.7)	2119 ± 489 (23.1)
Flipper length mm	165 ± 5.0 (3.0)	163 ± 5.1 (3.1)

respectively. These differences are significant, $P < 0.001$ and the values are 71 per cent and 83 per cent below those of the respective adult values given in Table 3.

The data for flipper lengths show that the yearlings in both samples (of mixed sexes) were short-flippered, having mean values closely approaching those for adult females. Neither sample shows any clear bimodality that might be linked to sexual differences.

The mean body weights for the Campbell Island yearlings exceeded those for either adult sex given in Table 4, whereas those for the Antipodes Island yearlings were below the adult values. These anomalies are again almost certainly a consequence of differences in the stages of the annual cycle at which the two populations were sampled. That from Campbell Island included 12 premolt "fats" with a mean weight of 3283 ± 213 g, whereas the one from Antipodes Island included only four similar birds (mean weight 3162 g) but also 19 molted ones ready for the sea that averaged 1884 ± 247 g and which account for a substantial proportion of the variability of that sample. These differences in weight emphasize the role of subdermal fat in tiding the birds over the molt when they are unable to feed and their body insulation is temporarily reduced.

Chicks

As sexual dimorphism evidently extends to yearlings it might also be expected to show in the dimensions of 72 chicks, almost or completely down-free and ready for departure, measured at Antipodes Island between 9 and 12 February.

The data for body weights and beak shape indices are given in Figure 6. Both polygons suggest the interaction of more than one normal distribution but with much overlap, as would be expected of animals actively growing, not of identical ages, and subject to variables like the differing capabilities of parents at finding and delivering food. The weight polygon has a rather extended tail of low-weight animals that would probably die before fledging. That for beak index appears to be bi- or even trimodal, with the peak between indices 300 and 400 difficult to explain on biological grounds and probably a consequence of inadequate sample size.

Table 6 gives the means and standard deviations for the various parameters when the data were treated as homogeneous. When the cumulative frequencies for weights were plotted on probability paper a change in slope around 1980 g suggested that the distribution can be explained in terms of two normal curves with 74 per cent of the birds lying in a light weight category around a mean of 1750 ± 180 g and 26 per cent being significantly heavier ($P < 0.001$) around a mean of 2200 ± 150 g.

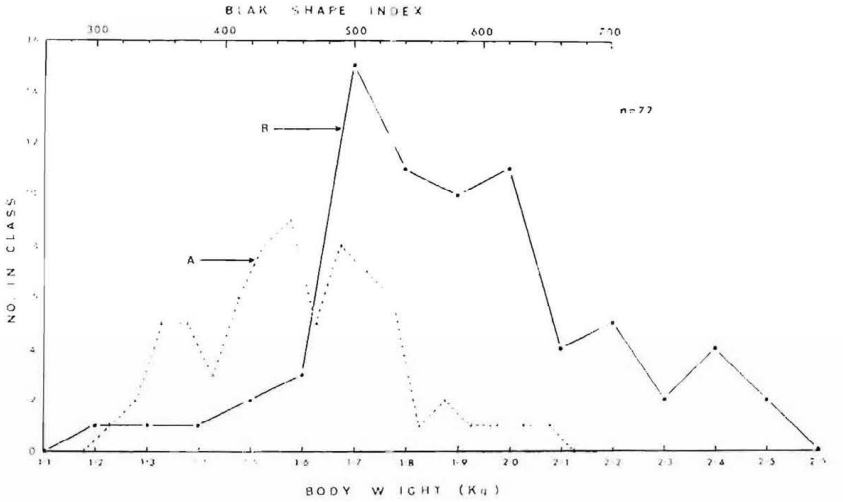

Figure 6. Beak shape indices (A) and body weights (B) of 72 Rockhopper chicks ready to fledge.

Data on beak shape indices are less amenable to further analysis but if the peak around 350 is ignored, the rest of the distribution can be explained as due to two normal curves where 60 per cent of the birds lie about a mean beak index of 410 ± 50 and the upper 40 per cent around one of 510 ± 35, values that are again significantly different with $P < 0.001$. Furthermore despite a lot of scatter, heavier chicks tended to have heavier bills ($r = +0.469$, $P < 0.001$).

Compared to a sample of adults of mixed sexes these near fledglings had bills that were 48 per cent as large whereas their flippers were 96 per cent as long so that the chicks evidently go to sea with their flippers better developed than their bills.

That the large-billed and heavy-bodied class were mainly males and the smaller-billed, lighter-bodied birds mainly females seems to be a reasonable hypothesis in view of the size differences among yearlings and adults. As the chicks could not be sexed by any other means and none was dissected, the existence of sexual dimorphism in bill size and body weight of the chicks just before fledging could not be proved, and the results can only be regarded as suggestive. Larger samples seem to be needed together, with corroborative data on sex based on separate characters, e.g. on the behavior of older birds marked and measured as chicks.

TABLE 6

MEASUREMENTS OF 72 ROCKHOPPER CHICKS AT ANTIPODES ISLAND

Bill length mm	38.2 ± 2.3 (6.0)
Culmen width mm	7.6 ± 1.0 (13.7)
Bill depth mm	15.3 ± 2.1 (14.0)
Beak shape index	445 ± 72 (16.2)
Flipper length mm	157.9 ± 19.4 (12.3)
Body weight g	1860 ± 268 (14.3)

DISCUSSION

Sexual dimorphism in bodily dimensions is rather widespread among colonial seabirds, being quite marked in penguins of the genus *Eudyptula* as well as in all five Eudyptids, in some petrels, e.g. *Macronectes*, and in many gulls. In *Eudyptes* it seems to be correlated with a greater aggressiveness by the males, but whether the dimorphism is maintained through selection pressures favoring nest defense, sexual recognition, the reduction of intraspecific competition for food, or serves other functions is unknown. Further comparative data from other species may throw some light on this aspect of the problem.

The data presented here support the idea that sexual dimorphism in the Rockhopper Penguin, starting perhaps in the chick, increases with age and is most pronounced among breeding birds. The age at which growth ceases is unknown and must await the repeated measurements of birds marked as chicks. Such a program would reveal whether the age at which growth ceases is the same for either sex and for each character, or whether bill size, for example, continues to increase even after breeding age is attained.

While the data reveal differences in bill measurements between the sexes of adults at a particular island, are the bill size differences between adults at the two islands really typical of their respective populations, bearing in mind that the data were collected at different stages in the breeding cycles? Significant differences in flipper lengths between the populations could not be demonstrated, and the figures for body weight ran counter to those for bill size.

When working with unmarked birds it is impossible to be sure that the adults measured at the two islands were drawn from strictly comparable age groups. Those at Campbell Island were still tending chicks, as were some of those at Antipodes Island, but others measured at the latter station were merely standing at nest sites with partners and either had no chicks or their chicks had left. Thus more of the birds in the Antipodes Island sample could have been prebreeders. If so, these, being younger, should have smaller bills and their inclusion would lower the mean value for beak shape index accordingly, whereas the means from this island are significantly greater than those from Campbell Island. Thus if such an effect is present it supports rather than invalidates the hypothesis that the breeders at Antipodes Island are heavier billed than those at Campbell Island.

The existence of minor differences in bill size between adults at Campbell and Antipodes Islands suggests that the gene flow between the populations is restricted, although the islands are only about 745 km apart. Such isolation is presumably in part due to the tendency

among Eudyptids for the young to return to their birthplaces. Other minor differences might therefore be expected to develop between such populations, and suggestive observations were made on one such feature, the extent of the pink coloration at the base of the mandible in the adult birds. In about 30 breeders of mixed sexes at Macquarie this pink mark extended forward from the fleshy gape for about one sixth of the length of the lower mandible and ended abruptly, clearly separated from the reddish brown of the rest of the beak. In most Campbell Island adults the mark was much more pronounced, extending from one third to one half of the length of the mandible as in birds figured by Bailey and Sorensen (1962: 106). In some Campbell examples the pink marking also extended along the proximal edge of the maxilla. At Antipodes a minority of breeders resembled Macquarie Island birds in this feature, but in most the pink was more noticeable and showed a condition intermediate between that seen at Campbell and at Macquarie.

Such minor differences suggest that careful comparisons using adequate samples from different breeding stations might reveal enough differences (in crest length and other mensural characters, underflipper patterns, etc.) to enable adults to be identified to particular populations. As the collection of long series is no longer permitted, at least on the New Zealand sub-Antarctic sanctuaries, it would be necessary as in the present study to rely on data drawn from live animals. Despite the obvious disadvantages, their use at least ensures that the data are free from uncertainties caused by shrinkage and fading that can complicate comparisons made from preserved skins, and live birds must in any event be used if repeated examinations of the same individuals are required.

Summary

The laying seasons at 11 breeding stations of the Rockhopper Penguin between 36° and 53° S were examined. Laying is roughly correlated with latitude, being earlier at the more northerly stations, but a better correlation is with mean annual sea temperature. The dates of laying advance about 10 days for each degree Centigrade rise in mean sea temperature. Marion Island appears to be exceptional in that laying is 8 to 10 days later than at other islands with similar sea temperatures. More precise information for many stations is needed to evaluate the correlation and to explain its underlying basis.

In an attempt to establish the degree of sexual dimorphism, culmen length and width, bill depth, flipper length, and body weight were measured in samples of adults, yearlings, and chicks about to fledge at Campbell and Antipodes Islands. No birds were dissected, but some were

sexed on behavioral characters found during a previous study to be specific for males. Bimodal distributions of the measured parameters were assumed to be the result of sexual dimorphism, and those birds sexed as males by behavior fell into the larger size category.

In 10 adult pairs the males were bigger billed and heavier than their mates, but some females had longer flippers. Data from 94 adults at Antipodes and from 59 at Campbell also indicated that the males were bigger billed and heavier. Males also had significantly longer flippers in the Antipodes birds, but this parameter showed more overlap between the sexes than did weight or bill size. Campbell adults were significantly smaller billed than those from Antipodes, and small differences were also noted in the bill color patterns of the two populations.

The 56 yearlings measured were smaller billed and shorter in flipper than the adults, but the bills and flippers of yearlings from the two islands were not significantly different. The 32 from Antipodes included a large and a small billed group believed to be males and females respectively, but none was dissected and behavioral clues to sex were not available.

The Campbell yearlings were heavier than those from Antipodes mainly because the Campbell birds included 12 in premolt condition (average weight 3283 g), whereas the Antipodes sample included many molted birds; 19 of these averaged 1884 g.

At Antipodes 72 chicks about to leave for the sea were measured. The data for weight and bill size were bimodal suggesting that sexual dimorphism in these parameters had already become established. These chicks' bills were only 48 per cent of the adult size, but the flippers were 96 per cent as large as those of the adults.

The function of sex differences in Rockhopper Penguin measurements is not known, nor is the age at which bill growth ceases. Differences in morphological characters between populations on different islands separated by wide stretches of sea probably reflect genetic isolation enhanced in part by the tendency of young birds to return to their natal islands.

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CHAPTER 4.

THE FIORDLAND CRESTED PENGUIN.

Eudyptes pachyrhynchus

C O N T E N T S

P L A T E S

F I G U R E S

T A B L E S

THE FIORDLAND CRESTED PENGUIN

Eudyptes pachyrhynchus

John Warham

INTRODUCTION

The Fiordland or New Zealand Crested Penguin, known as the Thick-billed Penguin in Australia, is a medium sized penguin standing about 40 cm high. It shows many similarities to its nearest relative, the Snares Crested Penguin Eudyptes atratus (= E. robustus). The Fiordland species differs from its congeners in lacking the fleshy edges to the bill plates which are prominent features of other Eudyptids and in usually displaying several white streaks on the otherwise dark cheeks.

This species nests near the sea in temperate rain forest on headlands and islands. It is a social rather than a colonial bird and when breeding congregates in small, loosely organised aggregations under cover rather than in the large, tightly-knit colonies in the open so typical of most birds in the genus.

Most Fiordland Crested Penguins breed on mainland New Zealand, principally in the bays, fiords and on offshore

islands along the west coast of the South Island below about 43°S. The breeding range extends along the south eastern coast of the South Island as far as Green Islets at 166° 40' E. Some also nest on the western and eastern coasts of Stewart Island but breeding groups appear to be rather uncommon there whereas they are plentiful at the Solander Islands further north at 46° 35'S, 166° 50'E.

The breeding season begins in the southern winter, ends in early summer and the birds are not seen ashore until the next breeding season, after leaving in early March following their annual moult. During the intervening 3½ months the location of the breeding population is unknown. Some birds evidently travel far. Immatures are fairly frequent visitors to southern Australia and Tasmania and there are Western Australian records (L. Nichols, pers. comm.). A specimen in the British Museum is labelled "Falkland Islands" (Serventy et al, 1971).

Two out of three birds taken from Jackson Head (43° 55'S, 168° 37'E) and released at Christchurch (43°35'S, 172° 45'E) were seen back at their point of capture subsequently, thus confirming the species' ability to home over considerable distances. Whether these birds swam back via Cook Strait (1,020 km) or via Foveaux Strait and up the Fiordland Coast (1,070 km) is unknown.

The biology of this bird has not previously been the subject of detailed study. Richard Henry (1903) described

some of the habits of the species in Dusky Sound, Fiordland and Sutherland (1920:1923) wrote about their breeding in caves around Preservation Inlet further south. He also described the young in detail at between one and 12 months old but as he did not explain how he aged the birds or whether these were retained in captivity during the autumn when they would normally be at sea, it is difficult to make much of his descriptions which contain many inconsistencies. Some of the differences between E. atratus and the present bird were set out by Falla (1935) who also gave particulars of its habits and breeding distribution. Oliver (1953) enlarged on the differences between it and the other New Zealand Eudyptids and (1955) gave a general account of its biology and status. More recent summaries of present knowledge are to be found in Falla et al (1966) and Serventy et al (1971). Stonehouse (1967) discussed aspects of the morphology and problems of heat balance in this and other penguins and included some further information and measurements of museum skins in a paper on the Snares Crested Penguin (Stonehouse, 1971).

The present account forms part of a study of the breeding biology of Eudyptids and comparative information for E. chrysocome, chrysolophus, sclateri and atratus will be found in Warham (1963; 1972); Warham (1971); Warham (in press); and Warham (in preparation) respectively.

METHODS

The research on the present species was conducted from 1966 to 1971 on birds nesting on the slopes of Jackson Head on the South Island of New Zealand. As it was impossible to spend a full 7 months in the field to follow events over a single season from the bird's arrival to their departure, the present account is based on observations made during repeated visits to the colony at various stages of the 6 annual cycles.

For individual recognition, birds were marked with numbered flipper bands. Initially these were made from soft aluminium strip which took a deep and easily read impression but which tended to erode quickly. They were gradually replaced by butt-ended stainless steel bands supplied under the New Zealand Banding Scheme. These resist corrosion well but the numbers are small and very difficult to read in the dim lighting prevailing within the forest. The bands were mainly fitted to adult breeding birds, but some chicks were also banded and in all about 260 bands were used.

The bands cannot be used on young birds until their flippers are large enough to retain them. When small chicks had to be marked paint was used and the webs were punched as Richdale (1957 : 183) did with chicks of Megadyptes antipodes.

A lone penguin when approached by man is often timid

unless it is sick whereas the same bird in the company of its fellows may be quite bold. Perhaps it is because so many Fiordland Penguins nest out of sight of others that they are so easily frightened by man. However, Falla (1948) records that when he landed at the Solanders the resident Fiordland Penguins "melted away" as he approached leaving a lone Snares Crested Penguin standing its ground, so perhaps timidity is an inherent characteristic of the present species rather than a consequence of its rather dispersed nesting habits.

The timidity varies from bird to bird and according to its activity and sex, the males being the bolder. An incubating penguin may allow a close approach, a moulting one will usually flee. A female will quite often leave its egg if approached by man when the male, if present, may then step forward and take over. Re-sightings thus tended to be biased in favour of the males, as it was impracticable to try to follow penguins that shift because they quickly disappeared into cover. This timidity also made it difficult to identify marked birds and to undertake the repeated examinations necessary when trying to chronicle events such as chick development and growth, as disturbance at critical stages can lead to mortality. Caution was also needed during banding. To lessen the danger of losing chicks or eggs much handling of the adults was done before laying and some during the moult. Breeding birds were not handled at all during wet weather when exposure might lead to the

loss of chicks and eggs. For similar reasons, no attempt was made to weigh particular individuals at intervals throughout a season to trace weight changes; instead, sample weighings were spread over all 6 seasons and the seasonal changes examined on the basis of the accumulated figures - see Appendix A.

Adult birds were weighed using a spring balance accurate to ± 30 g; chicks and eggs on spring balances accurate to ± 0.5 g. Egg dimensions were taken with vernier calipers and body temperatures with clinical thermometers accurate to ± 0.1°C inserted into the cloaca for at least one minute. Bill and flippers were measured as set down by Warham (1972). The foot measurements was the distance from the end of the middle claw to the back of the "heel". Other standard measurement were made according to the methods set out in Witherby et al (1940). Where appropriate, mean values for the various parameters are given in this paper ± one standard deviation. Mean values for data from large samples ($n > 30$) have been compared using standard error tests, from small samples using Mann-Whitney U-tests. Dimensions are of live birds unless otherwise stated.

A check was made of the changes in numbers of birds ashore by counting those seen during a morning traverse of the whole colony from a track running through it. Considering the variable conditions under which these counts were made,

they are reasonably consistent for a particular date from one year to the next.

In this paper a breeding bird is taken to be a member of a pair that has produced eggs during the season in question. Birds were sexed according to the sizes of their bills - adults with beak shape indices of less than 1300 being judged to be females, those with beak shape indices more than 1300 to be males (see later). Sexing was often confirmed on behavioural characters such as the positions of the partners during coition and the greater aggressiveness of the males, and on morphological grounds such as the larger size of one bird when members of pairs were together. Some birds found dead were dissected. These confirmed the reliability of beak size as an indicator of sex.

Prolonged observations on behaviour were made from a hide placed to overlook a group of nests.

THE BREEDING HABITAT

The nesting habitat of the Fiordland Crested Penguins at Jackson Head is probably quite representative of that selected by the species elsewhere. The birds occupy the lower slopes on the east, north and north-west facing sides of the promontory and nest from near sea-level to about 60 m above it. They are spread out along about 3 km of the coastline. An unmanned navigational light at

the end of the headland, commissioned soon after the start of this study, is reached by a narrow track through the forest and this has facilitated access to the nesting birds. The slopes are generally steep, averaging perhaps 45°, and rise into cliffs towards the Head. The birds land on beaches composed of large boulders and talus debris derived from the slopes above and they proceed inland along tracks that often follow the drainage channels. Only one of these carries water at all times but many other streams spring into life following the heavy showers to which the region is subjected at all months of the year.

Previously the birds also nested in the forest fringing the road leading east from the Jackson Bay settlement and some penguins were killed by traffic. However, road-widening and the resultant screes and slips have altered the character of the coast and destroyed most of the breeding sites so that few if any penguins now nest in these places.

The nesting slopes at Jackson Head are scattered with boulders of limestone, granite and conglomerate. The soil is dark and rich in humus but there are pockets of clay and a few small shingle fans. The slopes are covered by mature forest, the canopy height being about 21 m. The trees in the areas occupied by the penguins consist mainly of Kamahi Weinmannia racemosa, Rata Metrosideros umbellata, Tree Fuchsia F. excorticate, tree ferns Cyathea and Dicksonia spp.,

Broadleaf Griselinia littoralis, Pigeonwood Hedycarya arborea and Pate Schefflera digitata. The lower storey consists of bushes like Wineberry Aristotelia fruticosa and Mahoe Melicytus ramiflorus, and intertwined among these are the long, flexible, cane-like stems of Supplejack Ripogonum scandens and the tough, sharp-leaved Kie-Kie Freycinetia banksii. The ground cover is mainly composed of a wide range of Pteridophytes and there are beds of mosses and liverworts. The dense undergrowth, steep slopes, frequent gullies and fallen rocks make progress away from the access track difficult and fast movement impossible for a man.

The rainfall in this area is heavy but the amount of sunshine nevertheless quite high. At Haast, 45 km to the east of Jackson Head and the nearest station where records are kept, the average annual rainfall is about 364 cm and the annual sunshine some 1820 hours. Temperatures are quite mild. Stevenson screen data from Haast show that the average winter minimum there is about 4.0°C and the mean summer maximum about 17.8°C.

Within the forest the extremes of heat and cold are reduced. For example, while ground frost occurs in winter in exposed places outside the forest, the lowest temperature recorded within it during the course of this study was 0.6°C. Measurements taken at about 25 cm above the ground over 3 seasons showed that between the date of arrival of

the breeding birds in July and the departure of the chicks in late November and early December, the temperature never fell below about 2.2°C or rose above 15.5°C. In February, at the time of the annual moult, the temperatures were higher, reaching 19.0°C on one occasion. Throughout the year the maxima within the forest were 1 to 6°C below those outside and when the screen temperatures fell below about 5°C, those inside the forest were usually one or two degrees higher. The surface sea temperature in August during egg-laying is about 11°C rising to about 15°C in February when the adults are moulting.

The relative humidity inside the forest at 25 cm above the ground is usually close to 100% and is seldom below 80% when the penguins are ashore. The forest floor is usually wet, often saturated, but there have been short periods in mid-summer when the ground in places has been dry enough to make fallen leaves crackle under foot.

Although the vegetation and the network of vines and lianns impedes the human observer, they offer little barrier to penguin movement and in areas used by these birds tracks and foot-marks are numerous. The imprints of their sharp claws in the soft earth and scratches on the fine algal layer covering the exposed parts of the tree roots reveal the trails and activities of the penguins.

The nest sites are mostly in hollows at the bases of and underneath the roots of trees, beneath stones and boulders and within small cavities and caves in the clay. The

ground around such sites is generally so foot-worn that plant regeneration is impeded. Some birds nest on flat ground with no protection overhead but most birds breeding in the open lay their eggs beside a fallen trunk or against a boulder. Some find room within hollow logs and as the birds readily climb along sloping trunks they occasionally nest on top of these. One pair reared a chick in a shallow depression in the horizontal trunk of a huge Rata tree where the nest was about 10 m from the ground.

It has been stated that the birds seek the shade of the forest and subterranean nesting sites in order to escape the attacks of blackflies. This belief apparently stems from observations made by Richard Henry on Resolution Island at the beginning of this century (Henry, 1903). According to him the young ones stay in dark places to avoid the flies but come into the open to be fed and then the flies gather around them.

I have seen nothing like this during the course of the present study although blackfly attacks have been looked for many times. The area around Jackson Head is notorious for the abundance and virulence of its blackflies. Two species of Austrosimulium are involved - ungulatum Tonnoir, 1925 and australense (Schiner, 1868). These attack man freely whether he is in the forest or in the open. The insects readily take advantage of the biologist's pre-occupation to bite him when he is handling penguins but never, in my experience, bite the penguin!

The birds are well protected by their dense plumage and the flies are quite often seen resting or running over the feathers. The vulnerable places would seem to be around the eyes, on the feet and perhaps around the gape. The feet of resting birds are quite cold to the touch and must be well below the core body temperature; this may lessen their attractiveness to the flies. In the open, where the insects seem to be more active, the penguins appear to be unaware of the presence of biting flies and the birds often seem quite unhurried in their progress from the water's edge to the forest, even resting in the sun when the blackflies are numerous, particularly near the ground.

Only two instances of interactions between bird and flies were seen by me. A chick on 3 December was noted picking blackflies off its feet and a single blackfly was seen apparently probing the skin at the base of the bill of a moulting adult in February. In another incident, a field assistant reported finding an adult penguin on 11 January 1968, huddled in the centre of a swarm of what he believed were blackflies. The bird was injured and was dead the next day. The nature of the injuries was not specified but the flesh may have been broken and have made the bird more attractive to the insects.

Perhaps the blackflies to which Henry referred were of a species different from those at Jackson Bay: if not, they seem to have had different habits.

Plate 1: Fiordland Crested Penguins. The male stands guard over the first egg. The female has just returned to the nest after having moved away on the approach of the photographer and both are uttering throbbing cries which may lead to a trumpeted greeting ceremony.

CHARACTERISTICS AND MORPHOLOGY

The Fiordland Crested Penguin (Plate 1) shows many resemblances to the Snares Crested Penguin and rather fewer to the Erect-crested Penguin E. sclateri.

Fiordland Penguins have appreciably smaller bills than Snares Penguins but birds of equivalent sex and status must be compared as young birds are smaller than old ones and females smaller than males.

Otherwise, the most noticeable morphological difference from atratus is the absence of the fleshy fringes to the lateral bill plates present in other Eudyptids which culminate in triangular patches at the corners of the mouth. Instead the narrow skin in these areas is black.

The presence of white streaks on the black cheeks in many birds, to which mention has already been made, is a very useful character (Plate 1). Falla (1935) pointed out that this was a consequence of the feathers of the cheeks being separated to show their white bases. Short feather tracts appear to be disturbed by muscular action resulting in 3 or more stripes: in some birds however, these are seldom revealed. Conversely, a very few Snares Penguins possess similar white bases to the feathers and may show them as stripes during threat (Warham, in prep.).

Other morphological differences between atratus and the present species show more overlap. Both Falla (1948) and Oliver (1953) state that in E. atratus the yellow

superciliary stripe is narrower than it is in E. pachyrhynchus. This is only partially correct for while I have seen no pachyrhynchus with superciliary stripes as narrow as those of many adult atratus, in quite a number of the latter these stripes are as broad as they are in most pachyrhynchus. The variability in the thickness of the stripe in atratus is shown by the pair in Stonehouse's plate (1971, plate 1). The Snares Penguins generally have rather narrower stripes above the eyes which taper gradually to a point near the nostril. In the Fiordland birds the stripes are often broader and they usually narrow abruptly at the nostril.. Thus this is a useful but not diagnostic character. In both species the stripes tend to be narrower in females than in males.

The form of the crest is also variable. In adult Fiordland birds the long rearmost feathers tend to droop well below a line drawn along the tomia through the eye. Often the ends of the crest lie together so that it and the superciliary stripe create the impression of two curved yellow bars. More usually, however, the ends of the crest splay out laterally and may extend two thirds of the way across the cranium. The inner central feathers include many black ones but there is no real occipital crest as in the Rockhopper Penguin. In some Fiordland Penguins the tips of the black feathers on the occiput are white and produce a streaked effect.

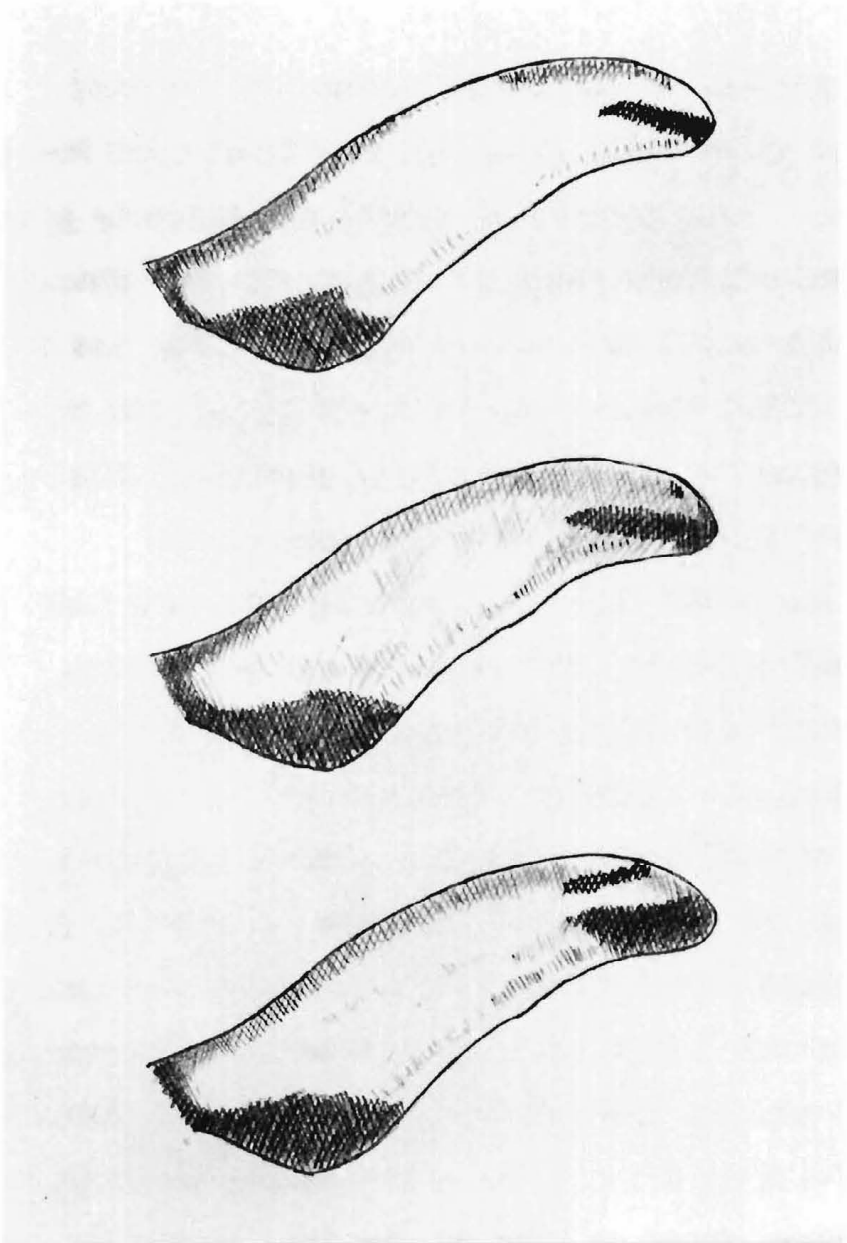


Figure 1: Underflipper patterns of adult Fiordland Crested Penguins. Uppermost is an unusually lightly pigmented example: the others are more typical.

The pattern of the under surface of the wing has been suggested as of value in separating Snares and Fiordland Penguins. Both Falla et al (1966) and Serventy et al (1971) figure underflipper patterns in Eudyptes but whereas the former show the Fiordland underwing as being the more heavily marked with black, Serventy et al show that bird's underwing as being more lightly pigmented. Figure 1 shows the normal range of pigmentation seen by me.

The Fiordland bird has generally the more lightly patterned underflipper, the stripe along the anterior margin being paler than in most Snares Island birds. There is a good deal of overlap between the two species in the patterning so that this is another useful, but not diagonistic character, if used alone. In both species the patch at the proximal angle of the wing has a brownish cast and when wet the whole undersurface is darker, the patterning less distinct, and the central area may be flushed with pink.

The bill of adult Fiordland Penguins is of the same reddishbrown shade as that of atratus, on the Munsell Colour Scale (Munsell, 1967) being from about 2.5YR 6/10 to 10R 5/10. It is a somewhat yellower shade than that of the eye. The difference is clearly shown in Figure 130 in Serventy et al (1971). Females often have slightly paler bills than those of their partners. Both sexes have their culminicorns bowed in outline when viewed from above and curving transversely across the base of this plate there may be low

arcuate ridges. These also occur on the bills of the chicks, and appear to be due to changes in growth rates. These markings are shown in drawings published by Buller (1905, 1: 89). Most breeding birds also have a series of narrow longitudinal striations at the base of the culminicorn imparting a grooved appearance to that plate. In males there may be as many as 15 such parallel striae extending forwards for about 8 mm. Females generally have fewer and shorter striations. The bills of Snares Crested Penguins often bear similar markings.

The flat, button-like eyes are generally described as being brownish-red in colour. Falla (1935) was more precise, calling them the "mineral red" of Ridgway. The colour of the eyes is actually rather variable and in breeding birds ranges from a dull brownish-grey just like that of the chicks (Munsell 10R 5/2 or 6/2) grading through a dull claret shade approximating to Munsell 10R 6/10, which is the commonest colour, to quite a bright vermilion (Munsell 7.5R 5/12 or 5R 5/12). In pairs, differences in eye colour can be rather obvious and a vermilion-eyed bird stays that way from year to year. Vermilion-eyed birds are quite common but most are males.

At the time of their arrival to breed Fiordland Penguins lack brood patches. However, there is an area of bare skin about 1 cm wide running from the vent along the carina to

the upper breast and it is on either side of this apterium that the brood patch develops. This seems to occur first in the males and by the time of egg laying the patch has expanded to become about 2.5 cm wide by perhaps 12 cm long in some of them. Most males have their brood patches developed to that extent by the time that incubation begins but in some the patch has still been quite narrow. By about 20 August all breeding birds of either sex have the patches well developed. There is little sub-dermal fat in this region and the patch tends to become recessed below the level of the surrounding skin and so forms a sort of pouch invested by feathers. The males at least seem to retain their brood patches right through the guard stage and into the post-guard chick-rearing period. Thereafter refeathering begins and in most adults of either sex inspected when feeding chicks in October and November the patch has reverted to its pre-breeding condition.

The brood patches of birds on eggs show their intense vascularisation by being of a deep bluish-red colour. In birds brooding chicks the bare skin is paler as well as usually being smaller in area.

Even at their full development the brood patches seem too small to embrace the two eggs completely. Nevertheless heat transfer cannot be inadequate as in many clutches both eggs hatch within a few hours of one another.

The body temperatures of the adult birds are low. A sample of 32 caught at rest had a mean cloacal temperature

of 37.65 ± 1.07°C. The 19 males in this sample had temperatures not significantly different from those of the females.

The vocabulary of the Fiordland Penguin is varied and complex. At sea a barking "haarg" appears to act as a contact note. Some of these calls are quite high-pitched and farcarrying, but others are composed of much lower frequencies. A high pitched cry, "the squeal", seems to connote alarm. Threats are accompanied by hissing, snorting and growling sounds, particularly from the males, who may give voice with higher pitched cries and harsh screams when fighting one another. Sexual displays like bowing are accompanied by explosive throbbing sounds while more complex displays involve elaborate pulsed braying calls with loud expiratory and inspiratory phrases. The males are the noisier sex.

At sea small parties may be seen "porpoising" along when travelling fast. Closer inshore the birds swim on the surface often with their tails cocked and make shallow dives as they move cautiously towards the landing places. If alarmed when about to leave the shore they scull away quickly, leaping from the water at intervals to help speed their departure.

In escaping from danger on land the birds run quickly without hopping, often holding their flippers slightly away from their bodies to assist their balance. If very

frightened they fall onto their bellies and drive forwards by thrusting feet and flippers against the ground. Such birds readily escape from men where the ground cover is thick.

In progressing uphill from the landing places, the penguins move in a cautious walk but they can hop quite well on level ground. Their feet have long, down-curved claws and the birds can use the tips of their bills to grasp irregularities when climbing. On descending, they examine steep places carefully before dropping down to land lightly on both feet, throwing their upper parts backwards at the same time to retain correct balance. The birds are usually well protected by sub-dermal fat and muscle so that quite severe tumbles are sustained without injury and one female that fell 7 m off a short cliff produced two eggs the following season!

NOMENCLATURE

In the present paper the Fiordland and Snares Crested Penguins are considered to be separate species. They are sometimes regarded as conspecific e.g. in a recent checklist of New Zealand birds (Kinsky, 1970).

Here I follow and agree with Falla et al (1966) and Stonehouse (1971). The latter gives as his reasons that the birds are distinct morphologically, without recorded

hybrids and that the breeding populations, though geographically close enough to be considered in contact, are reproductively isolated by breeding at different times of the year.

Some of the morphological differences have been outlined above and more precise quantitative data follow. I believe that the extent of the geographic contact has not been realised hitherto. On the Snares Islands each year, a considerable number of mainly yearling Fiordland birds comes ashore and moults in January and February. Upwards of a dozen land near the Biological Station and over the whole of the group it seems likely that hundreds may land to moult. They intermingle to some extent with the resident atratus but there is no evidence of any interbreeding, though this would be expected of birds only subspecifically distinct where the young, the most likely founders of new colonies, are in contact. In addition, some breeding stations of pachyrhynchus are quite close to the Snares Islands. Those at the Solanders are only some 160 km away and those on the east coast of Stewart Island perhaps a mere 125 km distant - only about 25 hours swimming time at, say, 5 k.p.h.

Would any such hybrids be detected? They might be difficult to recognise. At the Snares Islands, birds with incompletely developed fleshy strips around the bill have been looked for but never seen. The variability of the

TABLE 1. SOME MEASUREMENTS OF 20 PAIRS OF FIORDLAND CRESTED PENGUINS.

Mean values (mm) ± 1 S.D.

(Coefficient of Variation)

	Culmen Length	Culminicorn width	Beak depth	Beak Shape Index	Flipper length
♂♂	51.3 ± 1.74 (3.4)	12.6 ± 0.42 (3.3)	25.8 ± 1.63 (6.3)	1667 ± 172 (10.3)	185 ± 3.7 (2.0)
♀♀	44.0 ± 1.21 (2.7)	10.6 ± 0.48 (4.5)	21.9 ± 0.96 (4.4)	1022 ± 72 (7.0)	176 ± 5.5 (3.1)
$\frac{♂♂}{♀♀}$ x 100	116	119	118	163	105

underflipper patterns and the occasional atratus with white cheek stripes might suggest some gene flow between the two populations, but if it does occur it is insufficient to eradicate the constant differences separating the vast majority of individuals in the two forms.

The breeding seasons of the two species are well separated, the birds at Jackson Head laying some two months earlier than those at the Snares Islands. This is a considerable difference for populations breeding so near to one another and with no physical barrier between them. It is also probable that in Fiordland Penguins, as in some better known Eudyptids, the young birds tend to return to breed at their natal colonies: if so this will be a major factor tending to isolate the Snares from the Fiordland populations.

SEXUAL DIMORPHISM

As in other Eudyptids, adult male pachyrhynchus are larger than adult females. This is particularly well shown in the bill and a "beak shape index" obtained from the product of culminicorn length, bill depth and culminicorn width, measured as set out in Warham (1972), is of considerable value in sexing Fiordland and other crested penguins. Table 1 summarises bill and flipper dimensions for 20 breeding pairs of Fiordland Penguins. The larger-billed member

of each pair was considered to be the male. This conclusion was supported by these bigger birds' greater aggressiveness, by their being uppermost during copulation and by using the flipper action that precedes this act and which is not used by the females.

Among these pairs no female had any bill dimension as large as that of her partner and only two females had flippers slightly longer than his. In all the measurements the mean values for each sex are significantly different with $P < 0.001$. Occasionally a female weighed more than her mate, but this was a consequence of the long fasting spells which each undergoes in turn during the breeding cycle. Examination of the data in Appendix A shows that in sample weighings at various stages during their time ashore, the males always averaged heavier than the females.

Obtaining fat-free weights of these birds is impracticable so that comparisons of weights between the sexes are probably best obtained from animals weighed shortly after their arrival ashore following either their winter at sea or the post-nuptial period spent there, or at the conclusion of their annual moult. Of the data in Appendix A those for 11 July are the most relevant. The males were then about 13% heavier than the females ($P < 0.001$). Note the similarity of the mean weights of birds measured shortly after their arrival to breed with those of breeders on 8 February shortly after their arrival to moult.

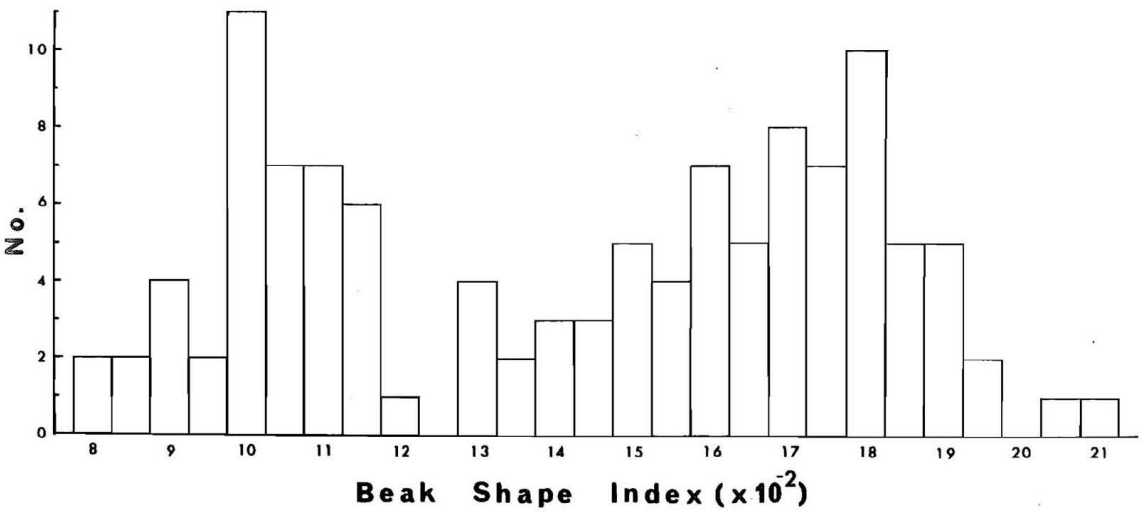


Figure 2: Distribution of the Beak Shape Indices of 114 adult Fiordland Crested Penguins.

TABLE 2. MEASUREMENTS (mm) OF LIVE ADULT FIORDLAND CRESTED PENGUINS.

	MALES		FEMALES			
	No.	Mean ± 1 S.D.	No.	Mean ± 1 S.D.	$\frac{♂♂}{♀♀}$ X 100	P
Culmen length	94	51.10 ± 2.01	61	44.97 ± 1.66	114	< 0.001
Culminicorn width	94	12.56 ± 0.59	61	10.61 ± 0.58	118	< 0.001
Bill depth	94	26.10 ± 1.66	61	21.84 ± 1.27	120	< 0.001
Beak Shape Index	94	1675 ± 183	61	1042 ± 108	161	< 0.001
Flipper length	87	185.7 ± 5.2	55	175.5 ± 5.8	104	< 0.001
Tail length	17	81.1 ± 6.9	17	83.1 ± 9.0	98	< 0.2
Foot length	32	124.0 ± 5.3	19	116.5 ± 4.5	106	< 0.001
Mid-toe & claw length	44	82.9 ± 4.0	34	77.3 ± 3.9	107	< 0.001
Crest length	15	44.9 ± 4.8	13	41.4 ± 4.1	108	0.10

The value of the beak shape index as a means of separating the sexes is emphasised in Figure 2 which shows the distribution of the values for this index in a sample of 114 adult birds, most of them breeders. Data from Table 1 are excluded.

This distribution is bimodal, there being no animals with indices in the range 1225-1275. The smaller size class is taken to be composed of females and the larger of males, a diagnosis that was confirmed in many instances by the birds' behaviour and occasionally, by dissection.

In Table 2 are summarised the values for various measurements made on a larger sample of adult birds, mostly breeders and again excluding those in Table 1. The sexes were separated on their beak shape indices, those with indices less than 1300 being classified as females.

Values for beak dimensions and flipper lengths closely resemble the means for breeding pairs in Table 1. It will be noted that the means for each parameter in Table 2 are significantly greater for the males than for the females except for those of tail and crest length. The males in the sample had, on average, shorter tails than the females but the difference is not statistically significant. Their shorter tails may possibly have been due to greater wear, as the males are ashore longer than the females.

The bimodality in the distribution of the values for the various parameters is greatest for those relating to

TABLE 3. SEXUAL DIMORPHISM IN SNARES AND FIORDLAND CRESTED PENGUINS.

	SNARES		FIORDLAND		
	No.	Mean (mm) ± 1 s.d.	No.	Mean (mm) ± 1 s.d.	P
Culmen length	35	59.1 ± 2.5	94	51.1 ± 2.0	< 0.001
	12	52.0 ± 1.8	61	44.9 ± 1.7	< 0.001
Culminicorn width	35	12.5 ± 0.6	94	12.6 ± 0.6	n.s.
	12	10.6 ± 0.7	61	10.6 ± 0.6	n.s.
Bill depth	35	28.2 ± 1.1	94	26.1 ± 1.7	< 0.001
	12	24.2 ± 1.1	61	21.8 ± 1.3	< 0.001
Beak Shape Index	35	2088 ± 186	94	1675 ± 183	< 0.001
	12	1332 ± 113	61	1042 ± 108	< 0.001
Flipper length	114	184.0 ± 5.1	87	183.7 ± 5.2	< 0.05
	82	178.8 ± 4.1	55	178.5 ± 5.8	n.s.
Foot length	12	114.4 ± 3.7	32	124.0 ± 5.3	< 0.001
	12	109.0 ± 2.6	19	116.5 ± 4.5	< 0.001
Mid-toe & claw length	42	78.4 ± 2.3	44	82.9 ± 5.3	< 0.001
	43	73.7 ± 6.0	34	77.8 ± 3.9	< 0.001

the bill. As birds with high values for beak shape index tend to have larger feet, flippers and crests, if the sexes are separated on the basis of bill size, as has been done here, then the values for these correlated measurements also show significant differences between their means although the overlap between the sexes is much greater than it is for beak shape index. For example, the flipper measurements show little evidence of bimodality in their distribution, some birds classified as females on bill size having long flippers and some males short ones. Nevertheless birds with big bills tend to have long flippers (the correlation coefficient for flipper lengths and beak shape indices from Table 2 is + 0.640; $P<0.001$) so that when the birds are segregated on bill size, the means for flipper length prove to be significantly different.

The means for the various dimensions are greater than those given by Stonehouse (1971) but as his figures were from smaller samples of birds of mixed sex, not known to be breeders, and were from museum specimens, comparisons are inappropriate.

Comparisons in Table 3 with data for live adult E. atratus from Warham (in. prep.) reveal some interesting differences.

The figures for the beak index show that in these samples the Snares Island birds averaged about 25% larger in the bill than Fiordland birds of the same sex. However,

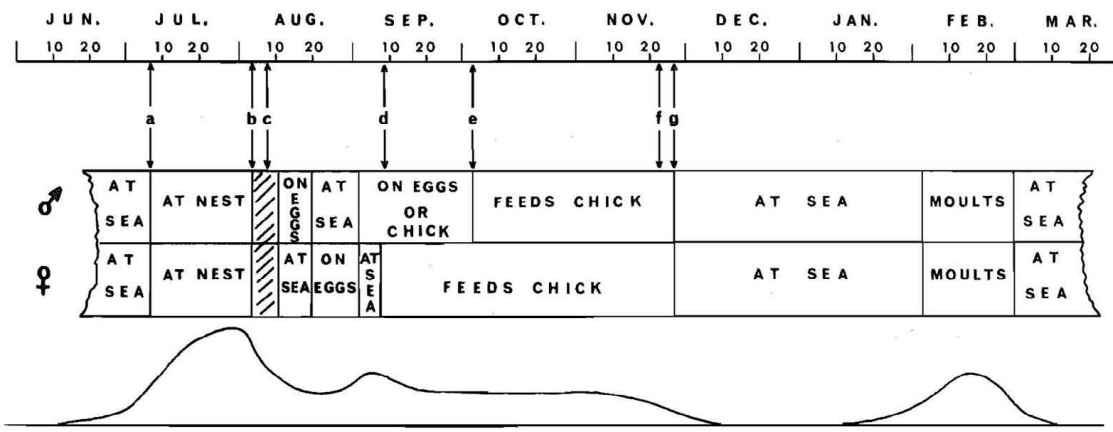


Figure 3: The annual cycle of a typical pair of Fiordland Crested Penguins showing a. arrival; b. & c. first and second eggs laid; d. hatching; e. chick enters crèche; f. chick departs; g. parents depart. During hatched period the adults change duties on the eggs frequently.
The graph shows the changes in numbers of all categories of birds in adult plumage ashore.

it will be seen that the Snares Penguins were bigger billed on account of these being longer and deeper. The culminicorn widths of the two species were the same. In contrast, the Fiordland birds had bigger feet. Why this should be so is unknown but comparative abrasion of the long claws in the different breeding habitats could be a factor here. Stonehouse (1971: Table 1) found no significant difference among his samples of skins of the two species in any parameter except culmen length and the length of the dorsal feathers - but his samples were of mixed sexes.

Unfortunately, I have no adequate data on body weights for the two species taken at the same stages of the annual cycle so that proper comparisons cannot be made of their overall size. The figures in Table 3 confirm what is clear from direct observation - that the most obvious size difference between the two species relates to the bigger bills of the Snares Island birds.

THE BREEDING CYCLE

a. GENERAL

The annual breeding cycle is spread over about 20 weeks from the bird's arrival early in July to their departure following the fledging of the chicks in late November. Figure 3 shows the routine of a typical pair and the graph below, based on track counts over 6 seasons, indicates the changes in the number of adult birds of all categories

seen ashore at the various dates.

It will be seen that the care of the eggs and chicks involves both parents in long shifts at the nest and that the male guards the chick for its first 25 days of life or thereabouts. During this time the female is solely responsible for feeding the chick. The male fasts. Thereafter both feed the chick until it departs in late November.

The birds breed annually and the timetable appears to be much the same from year to year but laying was slightly earlier in 1968. If the peak of laying is calculated as the date on which 50% of the nests in which eggs are laid have 2 eggs and 50% only one, then this stage was reached in 1968 about 1 August, whereas it was approximately 5 days later in the 3 subsequent seasons.

Richard Henry (1903) saw the first birds in 1900 on 16 July and in 1901 on 7 July. He collected 8 eggs from a cave containing about 50 pairs of penguins on 22 July that year. The birds breeding in this cave came ashore about a fortnight earlier than did other groups in the area. No similar variations between groups have been detected around Jackson Head. Henry's dates do not suggest that laying was very different in timing from that today at Jackson Head, 270 km further north.

Sutherland (1920) found the first chick of the year on 22 August 1919 in a cave in Preservation Inlet (about 340 km south of Jackson Head). This is the same as my earliest

date for that event. However, he also refers to eggs at all stages of incubation in the cave on 13 December 1919. If correct, this suggests re-laying, but as there are no confirmed reports of such an event in this or other Eudyptids except possibly for Rockhoppers at Tristan da Cunha (Elliott, 1957), and Sutherland made no mention of the eggs lost from nests that may lie around unbroken for many months, it seems advisable to reserve judgement on this episode.

Still further south, Falla (1948) saw adults but evidently no eggs on the Solanders on 20 July, and fully grown young there on 9 December. These dates suggest that the annual cycle at this station is much the same as that at Jackson Head.

b. ARRIVAL TO EGG LAYING

My first record of a bird ashore after the autumn absence is on 12 June and during the remainder of that month there is a steady increase in numbers. Males seem to predominate among the early arrivals although both sexes are represented. The numbers of birds ashore increase rapidly in July and more and more pairs are seen. By about 12 July something like 70% of the sites where eggs will be laid are occupied by lone birds or by pairs. By the end of that month nearly all sites have their attendant pairs and there are more birds to be seen by day than at any other time during their stay ashore.

On arrival the penguins are heavier than at any time while breeding. On 11 July 1969, 20 males weighed 4530 ± 373 g as against 17 females at 4026 ± 397 g ($P < 0.001$). For other weighings see Appendix A. The birds lose weight steadily thereafter and repeat sightings suggest that neither sex leaves to feed until after the eggs have appeared.

Newly arrived birds occasionally have Lepas barnacles about 1 cm long attached to their tails. These do not indicate excessively long periods spent at sea as has sometimes been supposed. Lepas 1 cm long would probably be only 3 to 4 weeks old (MacIntyre, 1966).

During the pre-egg-laying period the nests are excavated or re-made. Where the ground is soft enough it is worked into a shallow cup about 30 cm across by means of the feet and belly of the bird as it rotates in the nest. Many nests are lined with fern fronds and leaves pulled from bushes or with dead ones picked up from the forest floor, but the commonest items are sticks up to 40 cm long. Stones are collected when available. The males are the most active in this work and they may travel some distance out of sight of their partners in the search for suitable materials. Nevertheless, a typical nest contains very little lining material.

The birds are now rather timid and may leave their nests when approached. Those that remain may show their nervousness by shivering. There is a lot of calling,

particularly towards evening, and vertical head waving and vertical trumpeting displays are frequent, mostly being given by the males. If, as often happens, the weather is bad, the birds may get very muddy and bedraggled.

Coition occurs in early August and continues as late as 10 August between paired birds which have not laid. It appears to be restricted to a period of a few days before laying but was not seen very often during this study. On 4 August some lone males are still standing at nest sites apparently awaiting their partners, although many eggs have already appeared.

There is a good deal of fighting over nest sites during the pre-egg-laying period and some lone males try to form bonds with females which are already paired. This results in fighting between the males during which the female adds her harsh calls to the din made by the combatants.

By the time at which egg laying is at a peak - about 6 August - the birds have lost a good deal of weight. Nine males and 6 females which weighed 3556 ± 275 g and 3208 ± 226 g respectively on 4 August 1969 had lost about 21% of their weights 24 days previously. The period between arrival and the peak of laying extends over some 30 days.

c. PAIR BOND AND NEST SITE RETENTION

The pair bond in the Fiordland Penguin is one of sustained monogamy. Not enough breeding pairs were banded early in the study to provide good quantitative data, but

resightings of such pairs in later years indicate that a majority of them retained their bonds for at least two successive seasons.

Usually, when a bird took a new partner, its previous one was no longer seen. This does not necessarily mean that the missing bird was dead. It may have shifted out of the study area, to a subterranean site or elsewhere where it would be easily overlooked.

In two instances a change of partner is known to have occurred while the previous one was still alive. In both cases the females retained their original nest sites and their partners shifted to new ones with new mates. The original females acquired new mates themselves.

The nest sites also tended to be retained from year to year. At least 22 males and 9 females bred at the same nest for not less than 2 seasons, 6 males and 2 females for not less than 3 seasons, 4 males for not less than 4 seasons and 2 males for not less than 5 seasons. The figures are all minima and would probably have been increased substantially had more inspections been made on certain key dates.

Thus both site and mate tend to be retained. Five banded pairs bred at the same nest for at least 2 seasons and one pair has done so for at least 3 seasons.

Shifts of nest site seem to be more common than changes of partner. Often, such shifts are inevitable - the site may have been washed away, a tree may have fallen on it,

and so on. A number of shifts early in the study were of birds nesting close to or actually on the track leading to the lighthouse. The birds probably moved because of the disturbance (although few people used the track) or perhaps because in its preparation the canopy had been opened and allowed the sunlight onto the nesting places. One bird that nested here in 1967 shifted 2 m uphill in 1968 and a further 2 m in 1969 where it continues to breed.

Most shifts are usually over similarly short distances. The mean distance for 15 such shifts was 8 m, the longest moves being of 12, 20 and about 50 m. Thus, although it is probably true that most shifts are rather slight, long ones taking the birds out of the study area would most likely be missed.

d. EGG LAYING AND THE EGG

The first eggs are seen about 26 July and laying is complete by about 14 August in most years. The normal clutch consists of two eggs but in 10-20% of nests only one egg is seen. Probably in most such cases one egg is lost without the loss being recorded but some may be genuine single-egg clutches. Oliver (1955:71) indicates that on rare occasions 3 eggs are laid, but none of the many nests examined by me had more than two. Most pairs lay over a 10-day period between 30 July and 9 August. The peak of laying for 3 of the 4 seasons for which adequate figures were obtained was about 6 August. On or around that date about half the nests in which eggs were laid held one egg

TABLE 4. DIMENSIONS OF FIORDLAND CRESTED PENGUIN EGGS.

	No.	Length (mm) ± 1 S.D.	No.	Breadth (mm) ± 1 S.D.	No.	Weight (g) ± 1 S.D.	No.	LB^2 (cm) ± 1 S.D.
SMALL EGG	134	67.98 ± 2.55	134	51.86 ± 1.92	66	99.90 ± 7.82	134	182.8 ± 16
LARGE EGG	121	71.16 ± 2.30	121	54.96 ± 1.82	52	120.30 ± 8.62	121	215.0 ± 14

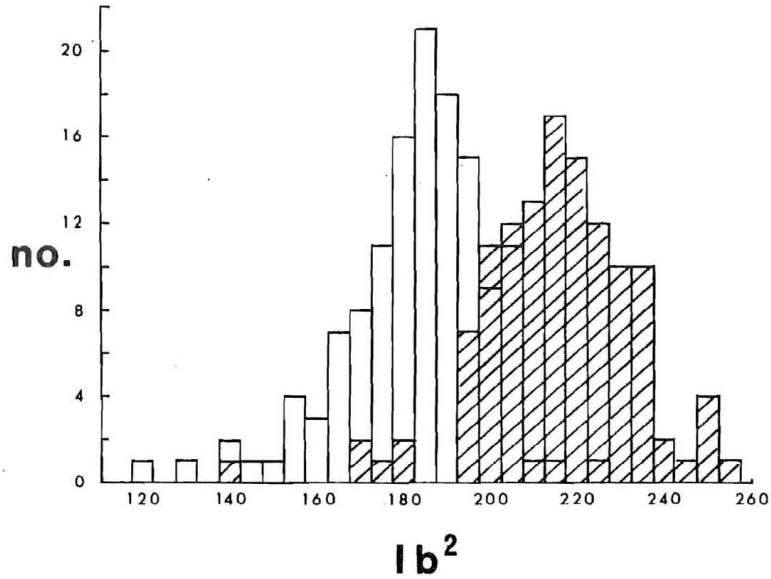
and half held two eggs.

The second, and larger egg is laid 3 to 6 days after the first, the mean difference in 10 instances being 4.1 days. Many eggs were marked as they were laid and in only once did the large egg (69.5 x 53.8 mm) appear before the small one (65.5 x 51.0 mm). This appears to have been a genuine instance of the large egg being laid first as there was no nearby and uphill nest from which a large egg could have rolled and have been added to the nest below. "Capture" of such displaced eggs is not unusual among more colonial Eudyptids.

The eggs are mostly of short sub-elliptical to short-oval shape in Palmer's (1962) terminology. More pointed examples approximating to this oval condition are also common. Freshly laid the eggs are a dull white in colour with a greenish or bluish cast, their surface matt and chalky with small irregular pimples. At the study colony they become stained brownish after about 2 days in the nest.

Measurements of a representative sample of eggs are given in Table 4. One dwarf egg measured 44.5 x 35.3 mm (33 g) and one abnormal clutch 41.5 x 49.0 and 51.2 x 68.5 mm. Such atypical eggs are not included in the sample from which Table 4 was compiled.

In this table the differences between the means are all highly significant. Values for length in cm x the breadth^2 in cm are given because these enable the weights of fresh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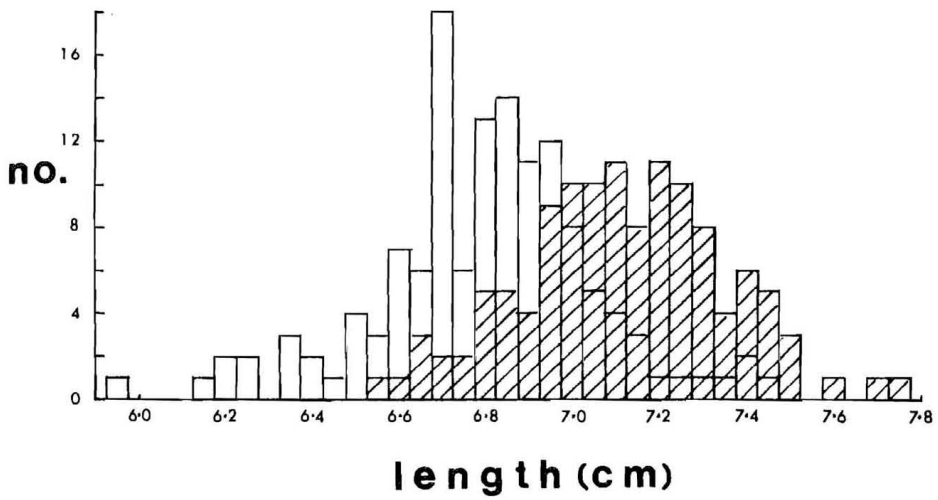
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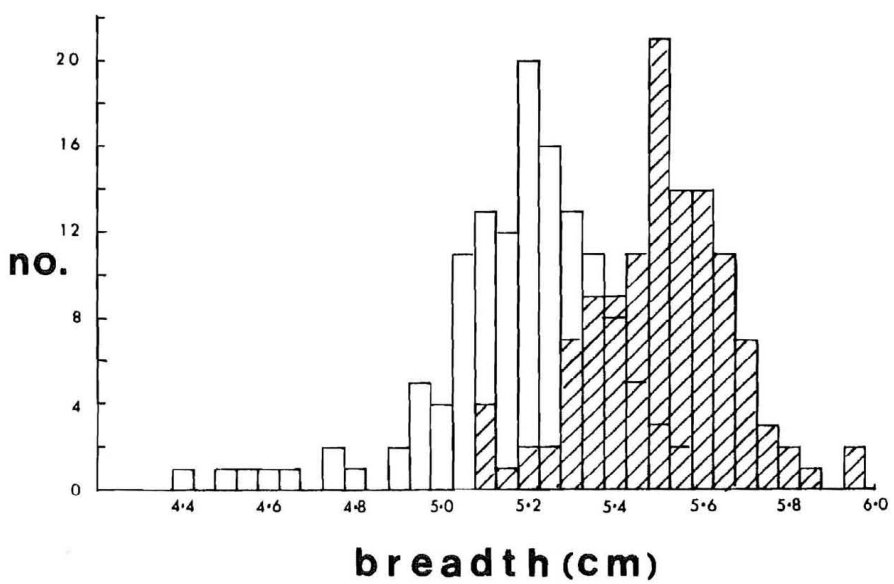
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breadth (cm)

Figure 4: Measurements of 121 large and 133 small eggs of the Fiordland Crested Penguin. The columns of data for the large eggs are hatched.

eggs to be calculated from their dimensions using the formula:-

$$W = k\ lb^2.$$

Using the weights of the 66 freshly laid small eggs and 52 large ones, "k" values of 0.551 ± 0.013 and 0.553 ± 0.010 were obtained. These means were not significantly different, indicating that the small and large eggs were similar in shape. The mean value of 0.552 can be used to calculate the fresh weights of short-oval eggs of this species. Eggs with "k" values of less than about 0.53 have been found to be pointed, part-incubated, or both.

The amount of overlap in the measurements for large and small eggs is considerable as examination of Figure 4 will show. Even if weights (or lb^2 values) are used it is still not possible to determine with a reasonable degree of certainty from its measurements whether a single egg was the first or last egg of its clutch unless it weighed less than about 108 g or more than about 116 g. However, within the clutch the difference is usually quite plain, the large egg averaging about 20% heavier than the small one.

The measurements in Table 4 may be compared with 50 clutches measured by Richdale (1950: 159). He gave mean values of 67.16 ± 2.4 x 51.73 ± 1.5 mm (92.82 ± 8.65 g) and 70.68 ± 2.1 x 55.37 ± 1.7 mm (112.76 ± 9.65 g) for the small and large eggs respectively. These were also from the Jackson Head area. His eggs were not significantly different

from mine in breadth but they were shorter, with $P < 0.05$ for the difference between the mean lengths of the small eggs and $P < 0.001$ for that between the means of the lengths for the large eggs. Even more divergent are his weights, which are significantly lighter than mine. A "k" value of 0.552 gives estimates of fresh weights of 99.2 and 119.6 g for eggs of the mean dimensions given by him. As the eggs appear to have been measured on 21 and 25 August the difference may be explained by their having had about 17 days incubation. Losing about 0.36 g per day (see below) their weights would have fallen to about 93 and 113.5 g, values which agree well with those he obtained.

The egg dimensions may also be compared with the mean values for a sample of 23 clutches laid by E. atratus (Warham, in prep.). These averaged 67.09 ± 2.57 x 51.05 ± 3.12 mm and 72.10 ± x 55.97 ± 1.24 mm. In neither dimension are the small eggs significantly different but standard error tests of the difference of the means show that the large eggs of atratus are slightly longer ($P < 0.10$) and significantly broader ($P < 0.001$) than those of the pachyrhynchus in my sample.

As with other penguin eggs the albumen does not coagulate when boiled. In 5 eggs measured the constituents averaged: shell 12.6%; yolk 25.1% and albumen 62.3%.

e. INCUBATION

Both birds are usually present throughout egg laying with one or other standing over the nest, but until the second egg appears the first is usually - but not invariably - quite cool when touched. Thus incubation proper does not normally commence until the second egg has appeared and then one or other of the birds adopts a prone position in the nest. The eggs are arranged with their long axes parallel to each other and the bird sits so that they are lengthways to its body.

The birds stay together for 5 to 10 days, and appear to take turns on the eggs during that time. The proportion of complete pairs at nests decreases from about 1 August while the proportion of lone incubating males increases. My figures for the period 10-20 August are scanty but it seems that in this species, once the rather extended period following the completion of the clutch is over during which both birds remain on duty, the females gradually leave, presumably to feed. The males thus take what is effectively the first incubation stint. This lasts for some 13 days from the date of laying of the second egg.

Thereafter, the proportion of males on eggs declines as more and more lone females are found incubating. Their numbers reach a peak about 23 August. This on-duty span for the females again seems to last about 13 days but there is a lot of variability. The males are not seen now and

are presumably at sea feeding after having fasted for 40 to 45 days since their first arrival. By the time that they leave their weight has dropped to about 3300 g, 73% of the mean value for males on 11 July.

With the females on the nests the breeding groups are rather quiet and there is little display activity. The nests are built up during wet weather and this may perhaps help to raise the eggs and lessen the chance of their being flooded out or displaced downhill.

Development of the eggs results in a steady loss of weight and for both large and small eggs this averages about 0.36 g daily. Thus a small egg weighing some 100 g when laid weighs about 88 g just before hatching, a loss of some 12%. Infertile eggs seem to lose weight at a similar rate.

From 31 to 36 days after the laying of the second egg the eggs hatch. For 13 instances the mean period was 33.5 days. Both eggs often hatch almost simultaneously, but 2 days frequently intervene. The first to hatch may be the first or second laid. My figures do not suggest that there is any regularity about this sequence. Presumably the fact that incubation does not start until after the second egg has appeared ensures that these hatch over a shorter period than that over which they were laid.

Eggs begin to be lost from nests from the very start of laying. Nevertheless the proportions of eggs lost to those laid seems to be lower in this species than is usual

among more intensely colonial Eudyptids, but I have no precise data to support this impression. Eggs that are displaced from nests are not recovered and soon get shifted downhill by gravity, particularly during heavy storms when the slopes become covered in a moving sheet of water. They are also easily lost from view down holes.

The events leading to the loss of an egg from a nest were never observed but I have no evidence that under normal conditions fertile eggs are ever deliberately ejected by the adults. On two occasions however, males have pecked at their eggs when I was removing them for weighing. I interpret this as being due to nervousness in my presence and of little relevance to their usual behaviour.

Egg shells, complete but for oval holes about 4 x 5 cm across and whose contents have been cleaned out, are quite often found on the ground away from nests in some seasons. The shell edges around the holes are cracked and turned inwards as though some animal has forced its way inside. In one egg, hairs adhering to the lining were determined to be of mustelid origin using the methods described by Day (1966). Possibly all the similar damage was the work of the same species. The size of the openings supports the belief that this was a stoat Mustela erminea.

In 1969, of a sample of 37 pairs that produced two eggs, 25 pairs had retained both up to the mean date of hatching, around 9 September. Some of these eggs were infertile or

failed to hatch for other reasons. The data for 1970 were similar but checks were not made during the peak of hatching. In a sample of 46 pairs known to have produced two eggs that season, 38 (83%) had still retained both by 4 September.

Only 15 discarded eggs were measured of which 8 were judged from their dimensions to be first eggs. This suggests that neither egg is lost more often although the small ones are subject to risk for 4 days longer than the large ones. Birds that lose their eggs soon disappear and relaying does not occur, but infertile eggs may be incubated for at least 3 weeks after they should have hatched and occasional eggs are found buried in nests as late as mid-February.

During the first week of September there is an increase in the proportion of lone males incubating and at hatching time the nests are either in charge of the males or both birds are present. Lone females are seldom on duty at this juncture. It seems that many males take charge of the eggs before hatching and are involved in a second and rather short stint of incubation. The females are missing at this time and are presumably at sea but no night-time checks were made, so that it is possible, although unlikely, that the females return to the nests at nightfall.

f. THE HATCH

Both large and small eggs are usually viable. Infertility is common and sometimes both eggs remain undeveloped, more often only one is infertile. This is just as likely to be the large as the small egg, but the sample sizes on which that conclusion is based are small.

Hatching is spread over much the same interval as laying, i.e. over some 18 days, and half of the nests with fertile eggs have produced chicks by 9 September and nearly all have done so by 17 September, the bulk of the chicks appearing between 4 and 14 September. The earliest chick I have seen was hatched on 22 or 23 August 1969. A very late one is estimated to have been born about 23 September 1971.

In 1968, 1969 and 1970, 78%, 69% and 89% of the pairs that laid produced at least one chick, a mean for the 3 seasons of 79%. Some chicks die shortly after hatching; indeed a few die in the egg at the point of hatching. Because tiny chicks that die often seem to disappear very quickly, it is difficult to follow the fate of chicks from large as opposed to small eggs. Chicks from either will die while their siblings survive. Likewise it is difficult to determine just how many pairs hatch both eggs, as the discovery of only one chick in a nest does not mean that only one has hatched, and as some parents, even at this stage, are prone to leave their nests when approached,

adequate checks are not always possible without serious risk to the delicate hatchlings.

g. THE GUARD STAGE

With the appearance of the chicks the male parents become increasingly in evidence at the nests. From about 36 days after the laying of the second egg and for another 3 weeks it is unusual to find birds other than males at nests still containing eggs or chicks, except towards evening when the females may join them. The males evidently fast throughout this guard stage. The only time that they leave the nest is when the female comes back, and then their excursions do not take them more than a few metres away as they search for items of nesting material. The weights of 11 males on 20 September 1969, had fallen to 2882 $\pm$ 368 g.

The newly hatched chick initially rests on its parent's feet and is tucked into the brood pouch like an egg but the parent tends to sit in a rather erect position. The chick seems quite weak but one 3 to 4 days old accidentally displaced was able to regain the nest 15 cm away by pushing with its flippers and feet. From the beginning it seems to be the female who feeds the chicks although the small chicks often beg unsuccessfully from the males guarding them.

The breeding groups are now quiet by day. The males pick up debris from within reach of their beaks and add it to the nest using a quivering action. Occasionally they

shift their position on the chicks which may thrust their heads from underneath the thick bed of feathers and wave vaguely upwards or may protrude their hindparts and defaecate over the rim of the nest.

The females reappear mostly from about 1500 hours onwards, their numbers increasing towards dusk. Some of them appear to feed after dark and they seem able to land at dusk and find their way through the forest when it is too dark for the observer to move without a torch.

The females are easy to identify. They are clean, wet and small billed, whereas the guardian males are splashed with mud and guano. On reaching their nesting group or another one through which they have to pass, the females adopt the "slender walk" posture with flippers thrust forward and feathers sleeked and on reaching their nests join in a greeting ceremony with their mates involving mutual head swinging and trumpeting. Thus the level of the bird noise in the forest increases towards evening as successive pairs, mostly unseen, are re-united. Some of these females do not remain ashore for very long once they have fed the chicks, and probably few remain all night, though this has not been adequately investigated. The chicks quickly put on weight (section i) and daily weighings of 7 chicks between 13 and 21 September 1969, showed that they were being fed almost every night, the mean period between 47 feeds being 1.1 days. Similar feeding frequencies seem to hold

throughout the guard state.

As the chicks grow, so the stance of the brooding males changes. The males become more erect and they show a thick belly-fold apparently due in part to loss of sub-dermal fat and in part to the way in which the brood pouch is inflated by the chick or chicks sheltering within. When the males stand up their thinness is shown by the way in which their thighs stand out, giving the birds a "trousered" appearance.

At about 18 days old the chick is usually too big to be covered and when danger threatens thrusts its foreparts between the male parents' legs leaving its hindparts exposed.

Some chicks die during the guard stage. In 1968, 1969, 1970 and 1971 of pairs that laid eggs 59%, 42%, 87% and 79% (mean 67%) respectively succeeded in rearing chicks to within about 7 days of the end of the guard stage.

h. THE POST-GUARD STAGE

At about 3 weeks old the chicks are no longer guarded. They are mobile and are found away from the nests huddled together in small groups or crèches. For a week and more before it leaves the nest to enter a crèche the chick moves around and explores the general area returning to the parent at night or when ever danger threatens. Crèche formation is a gradual process, starting about 20 September, and crèches are to be seen at all the larger breeding groups by a week later although many males are still on guard.

No accurate figures are available for the actual ages at which the chicks enter the crèches for the first time but there appears to be a good deal of variation here.

The guardian male is now at its lowest weight since coming ashore and soon departs to feed. Thus the gradual development of the crèches coincides with the gradual disappearance of the males. The females continue to feed the chicks, usually in the evenings, but sometimes earlier in the day. However, the disappearance of the male parents does not lead to any marked decrease in the numbers of birds ashore by day because many strange birds start to be seen, some of them paired. These are generally of unknown provenance, but are believed to belong to the non-breeding segment of the population (see below).

The weights of both adults tend to increase following the end of the guard stage: evidently the release of the male eases the load on the female and also allows him to regain some of the fat reserves lost during his long fast.

The behaviour of the parents on returning to feed their chick is much the same as that in other crested penguins. The adults return to their nests where they call and display, usually by bowing followed by forward and vertical trumpeting. If the chick is alive it soon emerges from a crèche or from concealment and totters to the nest waving its flippers and cheeping loudly. Then, continuing these actions and calls, it pecks towards the parent and induces

it to regurgitate. Perhaps 6 to 8 meals are delivered in due course, but often towards the end of the feeding period the parent tends to wander off the nest and a feeding chase of the parent by the chick results. Meals are then often delivered well away from the nest - perhaps as much as 10 m from it.

As the chicks get larger they wander freely over a wide area going up to 50 m from their nests. The crèches break down except for late-hatched young which may huddle together here and there.

In 1966 the break down of the crèches began about 14 October, but in most years this occurs about a week later. The crèches re-form if danger threatens, but the only enemy now seems to be man and introduced mustelids or perhaps, at some sites, interference from breeding fur seals Arctocephalus forsteri.

The males seem to take an increasing share in rearing the chick during November and it appears that after the ending of the guard stage the male is primarily concerned with self-feeding, but once having replenished some of its reserves, it can devote an increasing effort to the care of the chick.

The chicks may be fed at any time of the day but most still get meals in the evenings and even after dark. At that time they may be seen standing on nest sites that have been deserted during the daytime and each is on its own site.

Thus most parents find their chicks ready to be fed when they return. This tendency for the young birds to come back to the nest at nightfall was seen as early as 12 October.

Some early born chicks leave for the sea by mid-November but judging from the declining numbers seen in the study groups, the peak of departure is usually around 23 November. This gives a mean fledging period of about 75 days. No precise figures based on the departure dates of chicks of known age are available but the fledging period is likely to be much more variable than the period of incubation. Whether there is any marked variation from season to season in mean departure dates has not been ascertained.

The departure of the chicks is a gradual process and easily overlooked as the fledglings are seldom encountered at the water's edge. The departure of the adults, which seems to follow closely on that of the chicks, is also a gradual one. That an exodus is occurring is shown by the decreasing numbers of chicks and adults counted daily in the third week of November. A few late-hatched chicks may be seen, or more often heard cheeping, in evenings to about 5 December, but whether such late chicks succeed in fledging is unknown.

Little information was gained regarding the breeding success. On 13 November 1971, 26 chicks were known to be alive out of a sample of 32 that had been hatched in one area i.e. 81% survival based on one chick per nest. As a

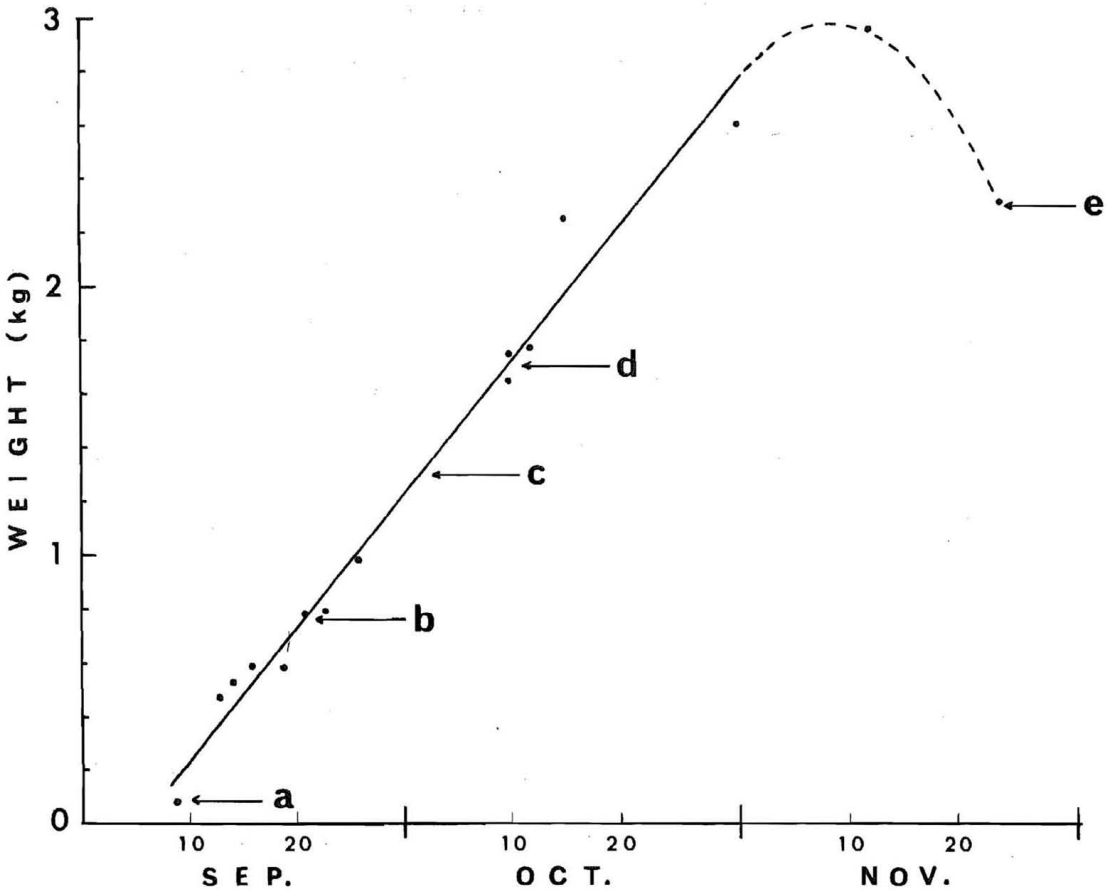

Figure 5: Generalised curve for chick growth in Fiordland Crested Penguins based on mean weights of randomly selected samples. Arrows indicate dates of: a. hatching; b. appearance of secondary down; c. entry of chick into crèche; d. appearance of tail feathers; e. chick departure. Trend line drawn by eye. Data from Appendix B.

chick had been produced during the 3 previous seasons in about 79% of the nests with eggs, then about 79% x 81% = 64% of the breeders may have succeeded in producing live chicks to 13 November 1971. Chicks continue to die right to fledging and being quite large are not so easily overlooked particularly as corpses attract blowflies. Probably in a normal year, about 50% of the pairs that lay produce swimming young.

The departure of the fledglings seems to present few physical difficulties in calm weather because the coast at Jackson Head is not invested with a belt of thick kelp such as penguins on the Snares Islands must negotiate. The only possible avian predators seem to be Kelp Gulls Larus dominicanus, but these have not been seen to take any notice of the young birds.

i. THE DEVELOPMENT OF THE CHICK

In the present study chick growth was followed by examining samples at intervals and a small sample of marked chicks was inspected regularly during their first 3 weeks of life. The pattern of the weight changes is shown in Figure 5, the data being given in Appendix B. Figures for the last weeks of the chick's stay ashore are scanty and the weight decrease preceding fledging is based on only a single late November sample, so could be atypical. However, the overall pattern of near-linear increase followed by a decline to fledging is similar to that seen in some

other crested penguins, e.g. the Rockhopper.

In this figure no allowance has been made for differences between chicks hatched from large and small eggs. When such freshly hatched chicks have been measured that from the large egg is usually about 20% heavier at around 79 g than that from the smaller egg at 66 g. However, a disparity soon develops and only one chick normally survives. Thus the data used for Figure 5 include chicks from both sizes of egg.

The regression line is drawn by eye and indicates a mean daily weight increase during the initial phase of about 50 g. Individual meals may be much larger than this and day to day weighings often show increases of 150 - 200 g.

The newly-hatched chick is blind and the rather sparse coat of primary down is of a dark chocolate-brown shade on back, head and throat and pale creamy white below and has a silky lustre. The bill is horn coloured with the culminicorn comprising the major part of the upper mandible, being convex from above and from the side. The nasal openings at the corners of the latericorns and culminicorn are prominent. The culminicorn has a few brownish streaks and the bases of the ramicorns and latericorns are blackish-brown gradually suffusing into the horn coloured area that extends to the tip. The egg-tooth persists as a pale pimple towards the tip of the bill. The feet and legs are pale whitish-flesh, the nails horn coloured but darker at their

sides and the distal ends of the toes are suffused with grey. The soles of the feet and the backs of the tarsi are a dull greyish-flesh. The flippers are covered with very short, fine down, so that they appear almost naked.

The eyes open after 4 to 6 days when the irides are seen to be dull brown colour. Growth is quite rapid, the bill lengthens and the horny areas become increasingly restricted as isolated patches toward the tips of the mandibles, the rest of the bill plates being glossy and blackish brown in colour. After about 12 days the mesoptiles appear at the bases of the protoptiles and soon fan out from the quills to form a dense fur-like coat that is blackish brown above and on head and throat and creamy white below but liable to much staining ventrally. A filament of primary down remains attached to that of the secondary down for some time before breaking off. There is a mid-ventral strip bare of down running up the belly from the vent. This strip is rather prominent in chicks whose stomachs are inflated with food. The fronts of the tarsi and feet are now pale flesh, the distal edges of the webs and the claws a mushroom-brown shade, the soles of the feet and the rear of the tarsi dull blackish-grey. There may be flesh coloured stripes along the soles of the innermost toes but usually the sole of the foot is black all over. The underflipper is covered with the same brown down as on the dorsal surface but a white central area of irregular shape soon develops.

By the time that the chick enters the crèche it still shows no feathers and the egg-tooth is still visible. This has almost gone by 10 October when the chick weighs around 1500 g and completely so by 20 October when it is some 40 days old.

At this age many chicks have traces of irregularly spaced ridges arcing around the base of the culminicorn which appear to be growth lines. There is often a slight median striation running forward from the base of this plate. Later, in many chicks, the arcuate ridges become more pronounced and several fine striations may also appear. The interior of mouth along the cutting edges of the beak is often of a peculiar yellow-green colour of unknown origin, not seen in the adult birds.

The first feathers usually appear in the tail and at the tips of the flippers. Thereafter the down is moulted from the underside and anterior half of the upper surface of the flippers, and from the lower back and underparts. Except for tufts of down at their bases the flippers are usually completely down-free before the body. The last down is usually seen attached to the feathers of the crown, on the nape and at the bases of the flippers.

Eruption of the rectrices starts about 8 October, when the chicks average between 1500 and 1600 g. These feathers have been about 60 mm long in the few fully feathered chicks that have been measured.

Plate 2: A male towards the end of the guard stage when the chick is too big to be brooded effectively. Note the pale cheek stripes.

The crest does not appear until feathering is well advanced on the body when it shows up through the overlying down as a narrow yellow supercilliary stripe about 50 mm long. By the time that the chick departs, sometimes with wisps of down still adhering to its nape, the stripe runs for about 8 cm from its origin near the nostril to the tip of the short crest. This is about 20 to 25 mm long, being yellow in colour but interspersed with blackish feathers. The rearmost crest feathers may either lie together to form a band continuous with the supercilliary stripe or may be splayed out at the rear, creating a spikey effect.

Newly feathered chicks are bluer and glossier than their parents, they are rather short in the tail, their bills with blackish-brown culmenicorns tipped with a horny patch about 10 mm long, the latericorns brownish anteriorly and the lower mandible blackish-brown proximally, browner towards the tip which ends with a horny patch about 4 mm long (Plate 2). The centre of the undersurface of the wing is whiter than that of the adult and the dark markings often prominent, so that the general pattern of the undersurface may appear bolder than it does in older birds. The throat and cheeks are grey due to their feathers having white tips and bases, black shafts and dark subterminal patches across the vanes. Some birds expose the bases of these feathers to form two or three tiny stripes - a character that would help to separate them from fledgling atratus.

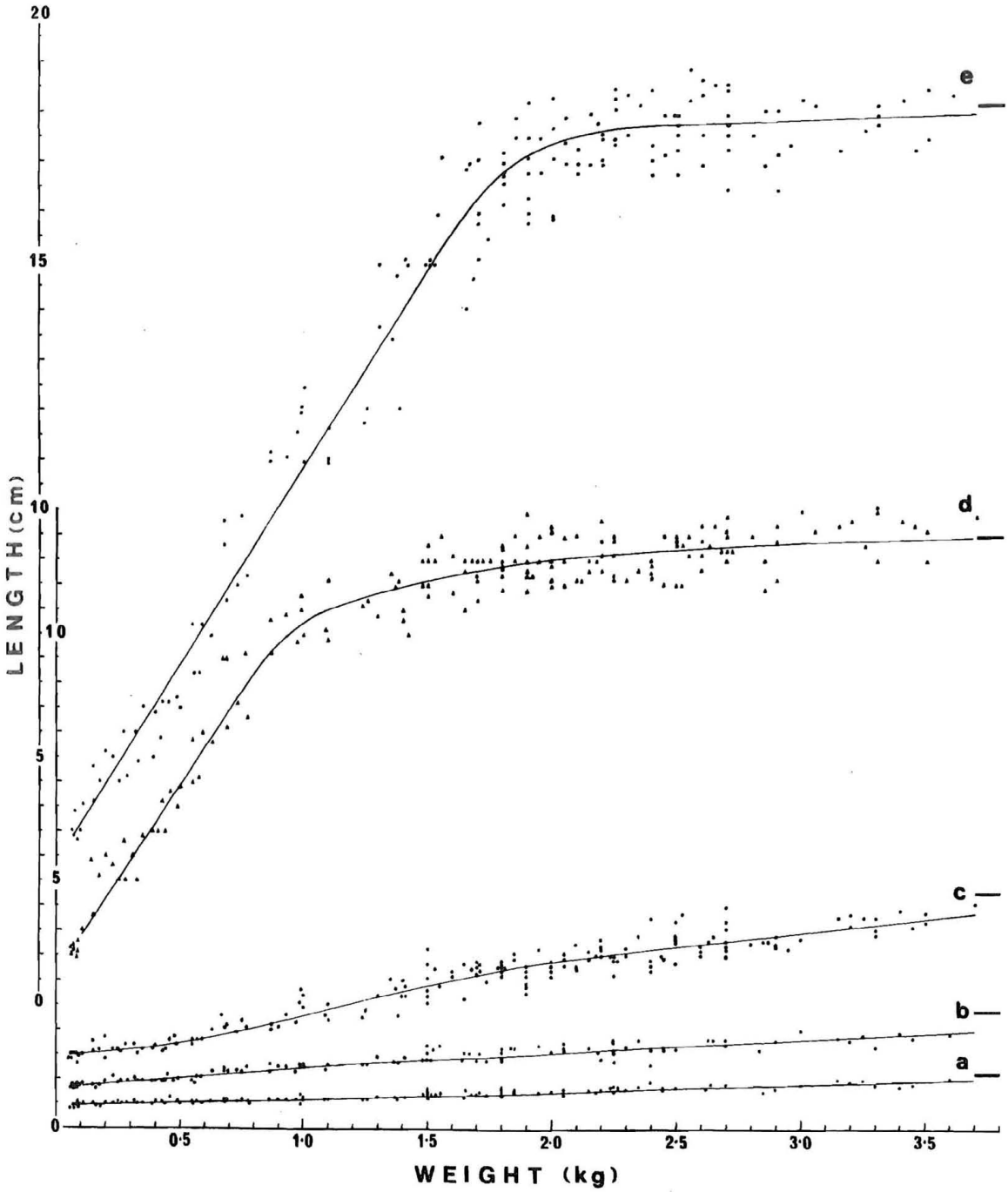
LENGTH (cm)
20
15
10
10
5
5
0
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
WEIGHT (kg)
e
d
c
b
a

Figure 6: Growth in Fiordland Crested Penguin chicks of various weights showing:- a. culminicorn width; b. bill depth; c. culmen length; d. foot length and e. flipper length. The scale for flipper length is offset by 5 cm from that against which the other lengths are plotted. Solid bars at right show mean values for samples of adult birds in which the sexes are equally represented and are taken from Table 2. Trend lines drawn by eye.

Figure 6 shows the lengths of flipper, foot and bill against body weight from 170 measurements of chicks taken in the 1967 and 1969 breeding seasons. There was no disparity in the measurements between the two years so that the data have been combined. Because it was impracticable to follow marked chicks and plot measurements against age, the above method of presentation has been followed. If the figures are plotted against the date similar curves result because, as Figure 5 demonstrates, there is a linear relationship between weight and date up to about 1 November.

It will be seen that whereas bill dimensions increase almost linearly throughout but never reach the mean size of those of adult birds, when they leave for the sea the fledglings' feet and flippers are about as long as those of the adults. Both fore-and hind-limbs experience a period of fairly rapid initial growth. At first the foot is longer than the flipper and the foot is about 90% of its length in the adults by the time that the chick enters the crèche weighing around 1300 g and must be fully mobile. The flipper is then still in the initial phase of linear growth and the rate does not level off until some time later. Similar growth patterns are usual in other penguins e.g. Megadyptes antipodes (Richdale, 1957: 55) and other oceanic species (Ricklefs, 1968).

3. TWINS

Both eggs are often hatched so that two chicks in a nest are not rare. Some idea of the frequency of this event are provided by data for 1968, 1969 and 1970. In these years 31%, 40% and 52% respectively of pairs still with two eggs in late August, hatched both. As tiny chicks often die and may disappear quickly the above figures are minima. Statistically, the differences between the years are not significant.

Freshly hatched twins differ in size in proportion as the size difference between the eggs. Very often one chick disappears or dies within one day of hatching and many are dead by the end of the first week. Sometimes both chicks die. As both chicks have not been marked immediately after birth the relative survival of those from large and small eggs, the effects of one hatching before the other, and similar factors cannot be assessed.

Generally twins are markedly dissimilar in size and when a chick dies it is nearly always the smaller one that succumbs. For example, twins at 12 and 36 hours old respectively weighed 59 and 131 g. Another pair aged 3 ± 1 day weighed 105 and 125 g but only one chick at 150 g was present one day later. Another pair at 7 ± 1 days old weighed 66 and 265 g and the smaller chick was almost dead. Normally single 7-day old chicks weigh about 550 g.

Twins that survive for 14 days or more are still of very

different sizes, but their combined weights may compare favourably with those for single chicks of similar age. Thus twins aged 14 ± 1 day weighed 575 and 1025 g as against about 950 g for single 2 -week old chicks. The eldest twins weighed, estimated to be about 19 days old, scaled 1200 and 900 g, a combined weight considerably above that usually achieved by some singletons known to be that age. Thus an important factor in twin survival may be the ability of the parents to provide a substantially greater amount of food than they would require to supply if rearing only one chick.

Despite the frequency with which both eggs are hatched in no instance have I gained any evidence that more than one chick from each nest survives to the post-guard stage. In some instances marked chicks have been watched being fed by their own parents and these have never fed more than one chick at a visit. In fact, late in the rearing stage it is seldom that more than one chick attempts to get a meal from a particular adult and if they do, only one succeeds. I conclude that it is most unlikely that in normal years any pairs rear twins successfully. The statement of Falla et al (1966: 25) that two chicks are frequently reared does not accord with my observations on this or on other Eudyptid. To prove that two chicks were reared would require marking these while still in the nest and following their fate to fledging.

k. FOOD

During feeding operations food tends to get spilled. In addition, food boluses are sometimes found on the ground. In nearly all such samples examined and in the stomachs of chicks that were dissected, the identifiable remains were predominantly of cephalopods. The exceptions were samples gathered in 1966 some of which were made up entirely of small Euphausids - probably Nictiphanes australis. Some quite large flukes and tentacles of squid have been found: one food bolus consisted of the complete tentacles and jaws of an animal whose longest arms were nearly 10 cm long. The jaws of squid are plentiful in the stomachs of chicks, often in association with eye lenses and long strands of elastic tissue. There may be hundreds of such jaws in a single stomach and the lengths of the hard parts of these jaws may vary from 3 to 10 mm in one bird. Whether this is because the food consists of different sized members of a single squid species or of different species is not known. Discarded food is often bright green in colour, apparently from bile pigments. According to Reischek (1884) young blue cod Parapercichthys colias are the principal food, but no identifiable fish remains have been found by me.

NON-BREEDERS

All crested penguins appear to undergo a long period of immaturity. In E. chrysolophus schlegeli, for example, a very few birds have eggs when 5 years old, most do so for the first time when between 7 and 9 years old, but some do not lay until 11 years old. The pre-breeders (birds that have never bred) come ashore as yearlings and when from 4 to 7 years old the males establish themselves at the breeding sites, attract females and in due course may become breeders (Carrick and Ingham, 1970). The pre-breeding segment of the population is thus of considerable size, and on the available evidence the situation seems to be similar in other Eudyptids. In E. chrysocome for instance, the pre-breeders become plentiful when the chicks are entering the creches and the males are leaving for the sea, and such birds infiltrate the colonies in the absence by day of the parents. These pre-breeders pair up and often occupy nest sites so that they can easily be mistaken for breeders and they may even interfere with the females when they try to feed their chicks, whereas the males soon put such interlopers to flight (Warham, 1963: 238).

Pre-breeders are also numerous in the Fiordland Penguin population but because few of them were banded and identifiable, the term non-breeders is used here to include both the pre-breeders and failed breeders without bands which

were again of unknown provenance. Some failed breeders are known to have spent a good deal of time ashore following the loss of their eggs or chicks. The yearlings, which are identifiable on plumage and bill characters, are excluded.

Birds believed to be non-breeders were seen ashore as early as 6 September and it is partly because of their arrival that the total numbers of adults ashore does not decline sharply following the hatch and the daytime absence of the females. These non-breeders are in adult plumage but tend to wander a good deal and may stand around well away from known nesting places often without partners. They are timid and difficult to approach. The presence of such birds is confirmed by the sighting in early September of two banded 3 years previously as chicks. These two appeared fully adult, with substantial crests. One whose bill was measured was clearly a male as its beak shape index was 1609. Its eyes were dark brown but the bill was as reddish as that of most breeding birds. On 12 October this bird weighed 3850 g but it did not appear to be ready to moult.

More non-breeders seem to be ashore during the post-guard chick-rearing stage in October and these have included at least one known 3-year old. Some of these birds form pairs, stand at nest sites and collect nesting material. Sightings of J 217 probably indicate the progression from pre-breeding to breeding status. The bird was banded as a lone,

rather small crested, male on 11 October 1966. It was seen several times that month at different places within about 40 m of the banding place. In the following season it was recorded only as a "pre-moult fat" on 24 February, and in the same general area as before. It was not recorded in the 1968 breeding season but was seen several times during the 1969 one in a breeding group about 150 m from where it was banded, but did not appear to nest that season. However, it did so in 1970 and 1971, being found with chicks in the same breeding group as in 1969. Thus this could well have been a 2- or 3-year old in 1966, which bred for the first time in 1970.

The only 5-year old sighted at the study area was seen as early as 27 August, so perhaps in this species there is a tendency for the pre-breeders to arrive successively earlier as they grow older until, when they are ready to nest, they come ashore with the established breeders.

The non-breeders disappear in late November apparently contemporaneously with the breeders and none has been seen ashore during the mid-summer hiatus in mid-December to mid-January. They are believed to moult in January and early February when the many birds found ashore away from nesting places and in adult plumage are presumed to belong to this category. No known-age birds, however, have been seen at this time.

YEARLINGS

Birds born the previous year are recognisable when they first arrive from early October onwards on account of their slimness, their brown bills often with blackish suffusions on the side plates, their brown eyes, white chins, and throats and cheeks more or less suffused or streaked with grey. Their superciliary stripes are rather broad but their crests are short.

Such birds are seldom seen in the study area, perhaps because they show little attachment to any particular place. They are likely to be seen anywhere along the coast. For example in January and February some moult in the culverts under the road leading from the Jackson Bay settlement and it is then that many appear on the Snares Islands (Warham, 1967).

The birds seen on the Snares in January are fat and 5 weighed then averaged 3766 ± 460 g. They tend to seek niches in rocks above the shoreline but some go inland and moult around the edges of the atratus colonies. Their plumage soon becomes loose and brown and the crests fade as the old feathers are pushed out and the moult begins. Completely moulted yearlings have been seen from about 25 January, but most are not seen until 5 to 10 February and occasionally as late as 20 February.

The yearlings lose their pale throats and cheeks at this moult. When they return to sea these areas are almost

uniformly greyish-black like the back but two or three whitish stripes are often exposed on the cheeks. These, and the absence of fleshy edges to the bill plates (although a little pink may show at the gape), and the smaller amount of black on the underflipper, enable yearlings of this species to be separated from those of atratus. During the moult the loss of weight is substantial: 6 moulted birds that were weighed before departure averaged 2177 ± 534 g.

ADULT MOULT

After the departure of their chick the breeding adults spend from 60 to 80 days at sea. The mean period, estimated from the rate of decline in numbers in December and the build-up in late January, seems to be about 70 days. The breeding areas and adjacent coasts are devoid of crested penguins from about 15 December until 9 January; the main body of the birds is absent for longer than this.

Successful breeders have been seen ashore at the end of January but most appear to arrive in early February. They are heavy with sub-dermal fat. Eleven males in this "pre-moult fat" state in February 1972 had mean weights of 4936 ± 350 g and 5 females in the same condition averaged 4820 ± 356 g.

Breeding birds are often found on the lower slopes asleep,

prone and facing uphill. Apparently these are newly landed birds resting before proceeding further. Most return to their nesting sites where they remain to moult if undisturbed. They are timid, fleeing readily if approached, and then often complete their moult elsewhere, though some come back to their nests later. The partners of breeding birds tend to join them at the nest site. About 5 to 7 days elapse before the old feathers start to fall commencing with the rectrices, during which period the dorsal feathers and particularly those of the cheeks take on a brownish cast and the crests fade.

The shed feathers pile up rapidly and the tell-tale accumulations may last for some time, indicating that birds have moulted on particular nests. But the birds are quite catholic in their choice of places to moult. They often perch on boulders near their nests and some must move about quite widely at this time because small piles of feathers with connecting trails are commonly seen. The absence of feathers at a nest site does not necessarily mean that the owners have not returned that season. Indeed, some well-established groups that share a common root-complex when breeding, persistently fail to return there to moult and are not seen again until the reoccupation of the sites at the start of the new season. I have been unable to determine in what way such neglected sites differ from apparently similar ones that are occupied at each moult by their owners.

About a fortnight elapses before all the old feathers have been shed but the bird is still without a tail and there is a delay of perhaps another week -sometimes more -during which the rectrices start to sprout and the body feathers lengthen, before the autumn departure to sea. Precise data from marked birds on the various stages of the moult are, however, lacking.

The moulted birds are thin, sometimes so wasted that the keel of the sternum stands out clearly beneath the feathers. The new plumage is grey-blue on back and head, the face tending to be greyer and there is little gloss to the feathers. The crests are bright yellow. The tail feathers are still far from fully grown when the birds depart, some measured at this stage being only about 3.5 cm out of the quills.

A sample of 13 males in completely new feathers but still short-tailed that was measured on the colonies averaged 3004 $\pm$ 289 g and 14 females averaged 2521 $\pm$ 227 g. However birds entering the sea would be even lighter than these. In this sample the males were 19% heavier than the females ($P < 0.001$) and some 60% of the mean weight of the sample of 11 males measured before the moult to which reference has been made ($P < 0.001$).

Although both members of a pair often acquire their new plumage at about the same time and both may disappear on the same day, it is not known whether they usually return to

sea together. Some birds are still unmoulted as late as 21 February but at the end of that month and in the first days of March the numbers ashore dwindle rapidly and after about 12 March no more are seen.

MORTALITY FACTORS

In this species mortality among the chicks is high bearing in mind that a considerable proportion of pairs hatch both eggs whereas none apparently succeeds in rearing both chicks. When twins are raised, one gets larger than the other and the dichotomy increases with time so that the death of the smaller in competition with its sibling seems inevitable. Whether food is ever abundant enough to enable any pairs to raise twins is unknown.

To evaluate the principal factors that lead to the deaths of single chicks requires further work. My routine checks suggest that a major determinant is the weather, in particular heavy rain leading to chilling. During the frequent gales in these latitudes the wind forces its way through the forest canopy and there are very few dry places anywhere at ground level.

The small chicks are probably ill-adapted to withstand any chilling but they are relatively easy to protect within the parent's brood patch at least in good sites. In bad ones such chicks may be drowned by flushes of water washing into the nesting hollow. The larger chicks may be almost

equally vulnerable. The penguin flipper, evolved for sculling the bird through the water, is ill-adapted for use in protecting penguin chicks during bad weather. Whereas many birds use their spread wings as umbrellas to shield their nestlings, a device that can be effective even against tropical downpours, the penguin flipper is unsuited to such a role and affords little protection for larger chicks. During the guard stage they may be able to find shelter for their foreparts beneath their parent but their hindparts often get saturated. During the crèche stage many chicks clearly get wet through.

The secondary down forms a dense coat that must be an effective insulator when dry because of the way in which the fine barbules that stand out from each barb loosely interlock with those from neighbouring barbs, thus trapping much air. But when wet the barbules collapse onto the barbs and these in turn tend to coalesce to form, in effect, a single hair-like feather of little if any protective value. The barbs quickly dry out in a dry atmosphere, the barbules separate and the original configuration is regained, but on the nesting grounds the air is seldom much below saturation point and in heavy rain a good deal of mud gets splattered onto the bellies of the chicks which further impedes the drying-out process.

Thus it might be expected that continuous heavy rain would be accompanied by increased mortality among the chicks.

Some data suggest that this is what happens. Thus September 1969, was very wet with rain falling every day between the 6 and 18 of that month. For several days the rain did not stop day and night and at times was very heavy. The continued rain coincided with hatching. In that year, of a sample of 31 pairs known to have hatched a chick, 12 had lost it by 20 September, a 39% loss. In 1970, however, in only one nest out of 64 where chicks hatched had the chick died by 23 September, a significant difference ($\chi^2 = 17.0$; $P < 0.001$). In 1968, 13 chicks in 53 nests where one was hatched had died by 23 September, a 24% loss. This ratio is lower than, but not significantly different from, that in 1969 ($\chi^2 = 1.0$).

Conditions at colonies of other Eudyptids are rather different. Most are more exposed and to colder winds than obtain in Fiordland but the annual rainfall is generally much lower, often falls as drizzle, and usually for shorter periods, although the lower precipitation may be somewhat offset by the presence of wind-driven sea spray. It may well be that the need to provide shelter for the chick is the dominant factor in the selection by many Fiordland Penguins of subterranean or other covered nesting sites. It must be admitted, however, that some established pairs, laying in the open without any real overhead shelter, still succeed in raising their chicks even in wet seasons.

The Fiordland Crested Penguin appears to have no natural enemies on land. New Zealand Fur Seals often share the same

rocky points and may well take some of the birds at sea but I have no evidence for that. Introduced Stoats and rats Rattus norvegicus are common in the area but only Stoats have been seen near the nesting groups and that rarely: in view of the dense vegetation they may be more common in the forest than is apparent. Some chicks have been found out of nests with their heads and necks chewed, their heads even severed from their bodies and occasionally with the viscera eaten. This may have been the work of Stoats. Mr D. Greaney (pers.comm.) related how a penguin fell from a bank to his feet with a tiny Stoat 7 to 10 cm long clamped onto the bird's thigh. The latter was evidently heading for the sea. The birds would seem to offer easy victims for these Mustelids but I have no other evidence for attack on adult birds.

The parasites of the Fiordland Crested Penguin include two Ixodes ticks, I. uriae and I.eudyptidis (R.L.C. Pilgrim, pers. comm.) and these are found on the chicks quite commonly in some seasons. In no instances has the infestation been heavy. In E. chrysolophus schlegeli some dead chicks have been found carrying such heavy infestations of I. uriae that these may well have been a major cause of death (personal observations).

During the course of the present study about 20 adult penguins have been found dead on the beach. The casualties have occurred from September to November and in January and

February. None has been banded and usually the cause of death has been obscure. Some have borne injuries of undetermined origin. Only one adult is known to have died in the forest.

The main causes of adult mortality and the regulators of population size in this species are unknown. Suitable breeding places do not appear to be limiting at least in the Jackson Bay area where well protected sites can be seen unoccupied every year. However, the Fiordland coastline is very indented so that its length is enormous and the penguin colonies, although mostly unrecorded, are probably numerous. Thus the total population, thinly spread along this extensive coast, may really be quite large. The situation is in marked contrast to that of other Eudyptids further south where land is scarce and crowding into vast colonies is the rule.

The numbers of the present species may well be in balance with the offshore food supply available within swimming range during the nesting season. On the other hand, the factors regulating populations size may operate outside the breeding season when the population is at its peak owing to the influx of the birds of the year.

DISPLAY BEHAVIOUR

Fiordland Crested Penguins employ a wide range of displays with accompanying vocalisations during their time

ashore. These are very similar to the actions and calls of other crested penguins like E. chrysocome (Warham, 1963) and particularly to those of E. atratus and E. selateri to be described elsewhere, so further detailed descriptions will not be given here.

This extensive repertoire seems to enable each bird to express its individuality. No two birds perform a particular action in precisely the same manner. Each has its own way of using its head, flippers and voice so that in combination a wide range of variations is possible. Some idiosyncracies are so marked that certain birds' voices quickly become familiar to the observer who may be able to identify an unseen caller and know just what display it is performing. Presumably such peculiarities help in individual recognition between the birds, important in long-lived species with a sustained pair-bond and highly aggressive males.

The voice is loud and carries well (except on stormy days with heavy rain) and there is clearly a good deal of mutual stimulation through these vocalisations even though the vegetation allows little visibility at ground level. Although most pairs nest within sight of only one or two others all are within hearing range of many of them.

The chicks have a restricted repertoire and their behaviour is like that of other young Eudyptids. Aggressive action by some members of the creches against their fellows

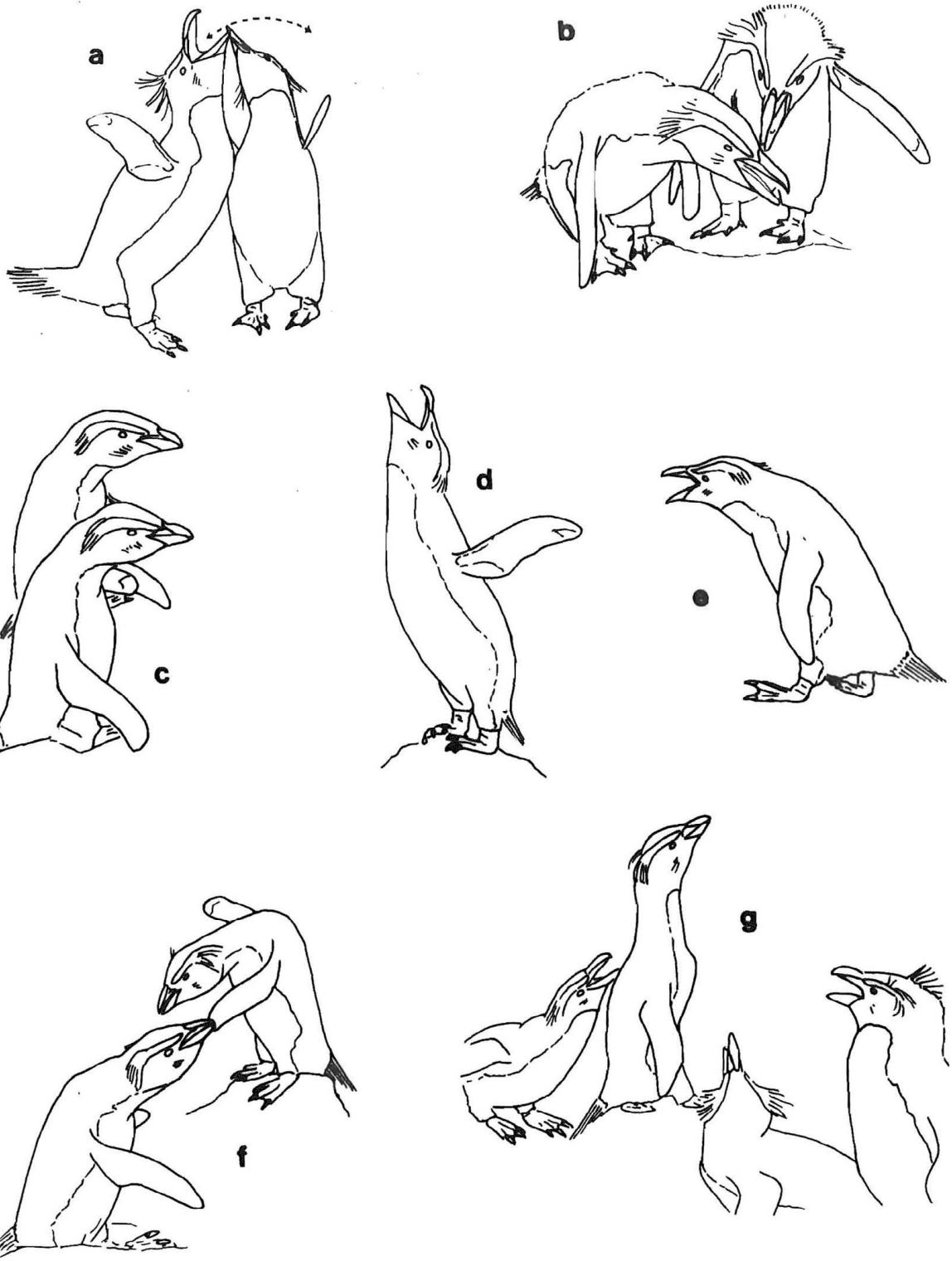
a
b
c
d
f
g

Figure 7: Some Display Attitudes of Fiordland Crested Penguins:-

a. vertical head swinging by a mated pair, the female on the right; b. mutual bowing into the nest; c. attitude adopted on seeing a man; d. vertical trumpeting by a lone male, the head is often swung even further back; e. forward trumpeting as a bird approaches its nest, the flippers are often swung forward; f. the shoulders-hunched attitude as a pair circle their nest site; g. the stare around posture of a bird which, in passing through a nesting group, pauses with head held high - the flippers are more usually thrust forward.

is common. The bill is driven into the back of the attacked bird and it is flailed with a flipper. Stand-up fights occur between more evenly matched chicks during which their bills may become interlocked. Timid towards man, the chicks often retreat to seek safety under rocks. One large chick standing at a nest adopted a strained attitude when it suddenly saw me, thrusting its head and flippers slightly forward as it moved away : this was apparently the start of the "slender-walk" posture.

Common and dramatic actions used by adults are vertical and forward-trumpeting (Figure 7 d,e). These displays are given both by lone birds and by pairs and the actions may be contagious between neighbours. Forward trumpets leading to vertical ones are the usual reactions of birds returning to nests after a considerable absence, and the displays and their accompanying vocalisations are the signals to the chick (if any) to return to the site. When the males are on guard they often initiate mutual trumpeting by calling and displaying when their partners are coming back to the nest but are still several metres away.

Paired birds typically perform the trumpeting displays when facing one another. The female may initiate the action by stretching up towards her partner uttering explosive throbbing sounds and then arching her neck and turning her bill down and away from the male. He then bows his head to throb similarly and then both swing their heads back

and up to trumpet vertically with deep measured braying cries and raised flippers.

Even more common is the vertical head swinging action (Figure 7,a) which in this species is not confined to the males as it is in E. chrysocome. Trumpeting and head swinging are often closely integrated. Many vertical trumpets end with short head swingings and even more often, head swinging, in which the head is shaken through rather narrow arcs so that the crest appears as a yellow blur, ends with a brief burst of vertical trumpets. The accompanying calls, however, are neither so sustained nor the pumping actions so pronounced as when vertical trumpets develop directly. Head swinging involves quite rapid oscillations of the head with bill pointed to the sky. The beat is slower than that of the displaying E. chrysocome, but rather faster than it is with E. sclateri and E. chrysolophus.

A mutual display like that of the Rockhopper is used by Fiordland Penguins and usually commences with the female bowing and throbbing into the nest while at the same time reaching towards her mate (Figure 7b). Their bills often come close together and hers may even pass inside his. Then the male swings his head into the vertical head-swinging display and ends with a short trumpet delivered on tiptoe while the female reaches up towards him without relinquishing her place on the nest. She accompanies him with

loud cries but in a voice that tends to be higher pitched.

When the female bows towards the male and often moves her bill from side to side, she behaves very like a chick begging for food. Her actions seem to have and irresistible effect on the male, causing him to throb and to bow in response. This seems to be the basis of the throbbing and bowing that occurs when a bird of either sex feeds a chick in the presence of the partner. As the parent bows down with drooping flippers to begin regurgitation, the other usually bows and throbs at the same time. This can distract the feeding bird, particularly if it is the female: it seems to be torn between the need to disgorge and the need to call in response to the other's display.

Most Fiordland Penguins defend their "individual distances" and their nests tenaciously when these are encroached upon by other penguins (Figure 7,g), the males being the more aggressive. Underground sites are particularly easily defended by determined males. Threat usually involves an arching of the neck as the head and bill are thrust forward. The hyoid is lowered and the flippers often swung forwards and spread so that a bird on its nest may rest them on the ground to help support forward jabs of these become necessary. Some birds make low hissing sounds when threatening in this way, backing these up with sudden lunges in which the bill is opened ready to grapple onto the adversary. Before striking, the head is often rolled to one side.

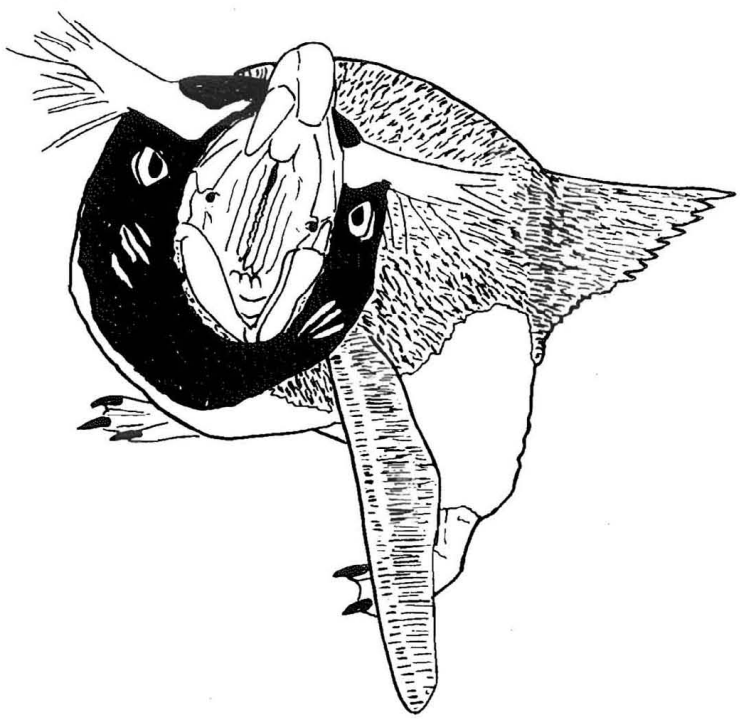

Figure 8: The reddish bill is emphasised when a Fiordland Crested Penguin lunges at a rival. The yellow crests lead the eye to the beak and this, and the wide expanse of pink buccal cavity and the white facial stripes, are sharply contrasted against the dark cheeks.

Most birds hiss at low intensity, utter deep growls and snorts at higher intensity, and if these are unsuccessful, their lunges are accompanied by loud yells. If fighting results the birds may get their bills interlocked and a tug-of-war may develop. The accompanying coarse screams carry far and are often followed by the sounds of beating as one bird wallops a series of flipper blows onto the body of the other. Birds that have been fighting often have the skin at the base of the bill torn away and nearby feathers missing. Fighting occurs throughout the bird's time ashore.

In other crested penguins the fleshy flanges to the beak appear to increase the communication content of threat, outlining the main offensive weapon, the bill. The present species does not have these pale flanges as the exposed skin around the bill is dark but most birds puff out their cheek stripes when threatening and these become rather striking when seen from penguin eyelevel (Figure 8). They may therefore fulfil the same role in the present species as the fleshy fillets appear to do in the others.

Trumpeting may also function as threat. At my approach a pair shifted close to the site of a neighbouring male. He stepped forward and challenged the intruding male by reaching towards it in a violent display of forward trumpeting. The challenged male responded similarly so that for several seconds the birds were face to face, heads and necks at 45°, their bills actually touching and flippers raised. The din

was deafening, as is usual in such encounters. Then the lone male deliberately turned its back on the intruder, stalked back to its nest, switch-to the "shoulders-hunched" posture, gave a short vertical head swing and relaxed. The pair meanwhile moved back to their own place.

The "slender walk" attitude is used by birds of either sex, as it is in other Eudyptids, when passing quickly and purposefully through a breeding group on its way to or from its own nesting place. The usual pauses to perform to "stare around" action (Figure 7,g) are also seen at this time. Birds that appear uncertain, e.g. one that returned to its nest to find that my hide had been pitched not far away, show this uncertainty by an excess of the jerky head movements associated with the "stare around".

Shivering is a common sign of nervousness and is induced by the approach of a human being. The bird does not shift and the action may involve not only the flippers but also tiny movements of the head as well. There is no correlation between occurrence of shivering with the ambient temperature and the movements cease once the observer moves away.

I have described in other members of the genus a rather puzzling vocalisation, a short, high-pitched squeal that lasts for about one second. This cry is generally heard in circumstances suggesting that the bird calling had suddenly encountered a frightening situation. In the Rockhopper Penguin, for instance, the squeal may be given when

a Southern Skua Stercorarius skua lonnbergi suddenly swoops across a colony. The cry may alert other birds nearby.

This cry is heard quite often among Fiordland Penguins and when the circumstances are apparent, it too seems to be the consequence of fear. The cry is heard throughout the time that birds are ashore, particularly when there are many at the nesting groups. Its greater frequency in this species may be due to their occupation of a forest habitat. Here a bird is more likely to be surprised by another than in the more open situations in which its congeners nest.

The squeal was heard in a variety of situations. For instance, penguins sometimes fight at the water's edge after arrival or before departure and squeals may be heard then. A male brooding a chick let out a sharp squeal in response to my sudden approach. There were several such instances but most squeals arise from encounters with other penguins. During watches from hides squeals were sometimes seen to alert other birds momentarily as evidenced by the sudden opening of the eyes of a dozing bird, a pause during self-preening, and so on. Squeals were often followed by the sounds of fighting but neither I nor the birds that were alerted could usually see what was actually happening.

A female, frightened by me, took shelter in a crevice where a male was incubating. He immediately attacked whereupon the female let out a series of very harsh squeals before breaking free. The cries appeared to have no effect

on inhibiting attack.

Another pattern of behaviour noted frequently in this species but seldom in other Eulyptids, concerns the reaction of a bird when suddenly sighting a man. A penguin moving through the forest suddenly seeing a man immediately stops, sleeks its contour feathers, often lowers its head until it and its neck is parallel to the ground, and peers hard, turning its head deliberately from side to side in a serpentine fashion as though judging the man's distance away. The bird may thrust its flippers forward and lift them so that they are parallel to one another, while continuing on its way if the person involved remains motionless.

This is the penguin's response to a motionless person. Of course, the bird could be detecting movements of which the observer is unaware, like those of the eyelids. However, during many such encounters I gained the impression that my presence aroused suspicion because I was a strange element in a familiar scene. The birds were often ones that as far as I know I had never seen before and which are unlikely to have encountered a man previously. Being long-lived, able to find their nests through a maze of vegetation despite a very restricted field of view, these birds must have an efficient visual memory of the routes that they use to and from their nests and the water. Their reaction to a motionless man may be a consequence of this memory and of

their ability to detect something alien in the well-known scene.

Although many females and some males covering chicks or eggs tend to crouch protectively over these when closely approached, I have only one record of the more complex submissive attitude being used by a Fiordland Penguin. An incubating female was found on her rightful nest with her bill hidden by being turned completely under her body. The cause was evidently the unbanded pair that was standing beside the female and that had probably been attacking her. The intruders were of unknown provenance but were probably non-breeders attempting to establish themselves in the nesting group. They shifted when I appeared and as a chick was subsequently hatched at this nest, their attentions cannot have disrupted the course of the nesting cycle unduly.

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SUMMARY

Aspects of the breeding and moulting of Eudyptes pachyrhynchus nesting on the west coast of the South Island of New Zealand were studied over 6 seasons. Nests occur in small scattered groups on steep slopes covered with heavy rainforest beneath which the birds are protected from temperature extremes.

The males are larger than the females. Figures are given for dimensions of breeding pairs and details of other morphological differences between the sexes and between members of the present species and its closely related congener E. atratus.

After about 4 months at sea the breeding birds return to land at the height of the southern winter. They aggregate in small, loosely organised groups, breed annually and tend to retain the same nest site and partner from year to year. They are ashore to breed for about 20 weeks before their chick departs. Incubation lasts for 33½ days and is undertaken in long shifts by both sexes in turn. It does not begin until the second and larger of the two eggs has been laid. The chick is guarded by the male for about 3 weeks during which time it is fed almost daily by the female parent. The chick then enters a creche and is thereafter fed by both parents until, at about 75 days old, it leaves for the sea. The parents also leave thereafter.

Details are given of egg dimensions and weights, of egg loss, rates of chick growth, the fate of twins and of the food brought to the chicks. Egg and chick losses are high. The heavy rainfall and frequent storms seem major sources of loss but the birds seem incapable of rearing more than one chick and when two are hatched a size disparity soon appears leading to the death of the smaller, apparently through starvation.

The adults moult annually in the forest, often on their nests, after some 60 to 80 days spent at sea fattening up for this event and they fast for about 25 days before their new plumage is sufficiently well grown to permit their return to feed. Their whereabouts out of the breeding season are unknown.

Display and associated behaviour are complex. They involve many dramatic attitudes in which the flippers and crests feature prominently accompanied by loud vocalisations.

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APPENDIX A. WEIGHTS (g) OF SAMPLES OF ADULT FIORDLAND CRESTED PENGUINS AT VARIOUS DATES.

	MALES		FEMALES		
	n	Mean ± 1 S.D.	n	Mean ± 1 S.D.	$\frac{♂♂}{♀♀}$ X 100
11 Jul. 67	20	4530 ± 373	17	4026 ± 397	113
20 Jul. 67	11	4473 ± 405	9	4144 ± 244	108
29 Jul. 69	4	3662	3	3367	109
31 Jul. 71	6	3700 ± 266	7	3414 ± 175	108
4 Aug. 69	9	3556 ± 275	6	3208 ± 226	111
23 Aug. 69	4	3325	9	2861 ± 312	116
20 Sep. 69	11	2882 ± 367	2	2475	116
24 Sep. 68	16	2716 ± 265	4	2612	104
11 Oct. 66	8	3096 ± 354	4	2762	112
4 Dec. 66	5	3285	4	3199	103
8 Feb. 72	12	4646 ± 655	8	4137 ± 911	112
15 Feb. 72	14	3461 ± 898	11	2854 ± 645	121
25 Feb. 68			4	2387	